Strategies of Protected Area Use by an Ecosystem Engineer

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Abstract

Protected areas (PAs) are necessary for conserving animal populations amidst human expansion, but may be insufficient for fully accommodating the needs of wide-ranging species. Animals' use of space and PAs may vary by age, life-history and social considerations. We quantified sightings and behavior of 516 adult Asian elephants from both sexes, over 9 years, to investigate how life history traits and behavior influence PA use at Udawalawe National Park, Sri Lanka. Male PA use, quantified in terms of average between-sightings-interval (BSI), was significantly influenced by the interaction of age class and motivational state (i.e. reproduction vs. foraging). A minority of males (11%) used it exclusively during mate-search, while the remainder used it exclusively for foraging (44%) or both (45%). Females' average BSI was significantly yet weakly influenced by social ties, indicating that members of social communities do not necessarily disperse together as a unit. Inter-annual variability in sightings among individuals of both sexes indicates that over half of the population are likely non-residential, challenging the dominant fortress-conservation paradigm of wildlife management in many parts of Asia. Our observations underscore that elephant populations in PAs may be more heavily dependent on adjacent landscapes than hitherto acknowledged.

Introduction

Global conservation goals typically emphasize setting aside land for wildlife (Butchart et al., 2015). Protected areas (PAs) can serve as refuges from anthropogenic impacts, both direct (e.g., harvest, hunting) and indirect (e.g., habitat modification). While much research has been devoted to developing metrics for prioritizing areas to protect on the basis of biodiversity or ecosystem services (McDonald-Madden et al., 2009; Corson et al., 2014), there has been relatively less emphasis on species' behavior (Caro & Berger, 2019). Indeed, some PAs may not meet conservation needs for certain taxa (Barnes et al., 2015; Watson et al., 2016) because globally PAs exhibit selection biases toward areas of low agricultural value rather than inherent ecological value (Joppa & Pfaff, 2009). Animal populations within PAs are also impacted by habitat degradation and activities outside PAs, as many species range beyond reserves (Runge et al., 2014); a salient consideration for large mammals. Despite offering important cultural and economic benefits, dedicated reserves may not suffice to protect wildlife (Thirgood et al., 2004; Craigie et al., 2010; Geldmann et al., 2013; Runge et al., 2014). Factors such as age, sex, and social status impact space use, interact with other life history traits, and can differ across the annual cycle. What fraction of any given population of threatened species actually relies on the PAs? How does PA-use relate to life history? Such considerations are as important as species or ecosystem diversity when designating and managing PAs (Beresford et al., 2011; Caro & Berger, 2019)

Animal movements link PAs with wider landscapes (Hansen & DeFries, 2007). We examine the PA-use strategies of a widely-distributed ecosystem engineer, the Asian elephant (*Elephas maximus*). Elephants move seeds, soil, and nutrients, influencing community structure (Haynes, 2012; Terborgh et al., 2018). Space use varies among species, habitats, and regions (Galanti et al., 2006; Williams et al., 2020), as well as between life history stages and throughout the annual cycle (Stokke & Du Toit, 2002; Fernando et al., 2008). PAs in Asia tend to be small, with 80% of those in South Asia being < 100 km^2 (Chowdhury et al., 2022), but they can be very important for wildlife when managed in conjunction with surrounding landscapes (Goswami, Sridhara, et al., 2014). Unfortunately, they often have low connectivity (Santini et al., 2016). Despite evident mismatch between the scale of elephants' habitat requirements and the scale of PAs in Asia, how elephants actually use PAs in relation to life history remains poorly understood.

Being a polygynandrous species with a slow reproductive rate, adults of opposite sex do not consistently associate with one another (Keerthipriya et al., 2020). Mature males alternate discretely between periods focused on foraging vs. mate-search/competition, which we refer to as *foraging* or *reproductive motivational state*, respectively. The latter consists of an annual state of heightened sexual activity, accompanied by altered hormone profile and increased movement, that is asynchronous among individuals, also referred to as "musth" (Jainudeen & Katongole, 1972; Fernando et al., 2008; Hollister-Smith et al., 2008; Keerthipriya et al., 2020; Taylor et al., 2020). The degree to which males use PAs for each purpose is unclear. Adult female Asian elephants exhibit fission-fusion social relationships persisting across years, even if not associated day-to-day (de Silva et al., 2011; Nandini et al., 2018). Relationships shift seasonally but lack the cohesiveness and stratification of African savannah elephants (de Silva & Wittemyer, 2012; Nandini et al., 2017). Their ability to move is an important mechanism for avoiding direct competition and conflicts, as dominance hierarchies appear largely absent (de Silva et al., 2017). Although social partners by definition have to be spatially associated at least some of the time, it is unknown, whether affiliates in fact use the same areas as one another long term.

While studies tracking the movements of individual animals provide perspective on home range attributes, they are typically limited in terms of the fraction of the population sampled and the duration of study. Using longitudinal data from direct observations of wild Asian elephants at Udawalawe National Park, Sri Lanka (Fig. 1), we investigate PA-use according to separate considerations for the two sexes. For adult males, we examine whether individuals preferentially use the PA for foraging vs. mate search, hypothesizing that area use would be structured by age and motivational state. For adult females, we hypothesized that PA-use would be influenced by the strength of associations among social affiliates. We first quantify the degree to which elephants revisit the PA over multiple years and then evaluate the influences on area use strategies for

each sex. We discuss how these findings complement recent studies from other parts of Asia and suggest a re-evaluation of the function of PAs for this and other similarly mobile species.

Results

Male PA-use

We identified 379 individual males during the six-year study period (Figure S3), with those seen in musth distributed across age classes and overall number of sightings (Figure S4). Of these, 216 were already mature (≥ 21 years old), whereas 25 that transitioned into maturity during the study and were excluded from analyses. Of the 216 mature males, 99 were seen only foraging, 94 were seen in both motivational states and 23 were seen only in musth. Those seen in musth were least likely to be seen across all six years of the study, whereas those seen in both states were most likely to be seen across years (Table 1). Those seen only foraging were largely split among those seen only in one year (38.4%) and those seen in all six (11.1%). Younger males were significantly more likely to be seen only foraging whereas prime-aged males were more likely to be seen in both states (Fisher's exact test $p < 0.0001$), with the propensity to be seen in musth peaking in the 31–40 age class and declining thereafter (Fig. 2A). Musth duration lengthened with age (Fig. 2B). Males seen in both states were more frequently seen in early-phase whereas males seen only in musth were seen slightly more frequently in the peak- and late-phases (Fig. 2C).

Table 1
– Number of mature males (≥ 21 years) using each strategy across years. N = 216 (musth-only (m) = 23 (11%), foraging-only (f) = 99 (45%), foraging & musth (f + m) = 94 (44%)). Musth-only males are the least reliably seen across years whereas those seen in both states are most often seen across years.

Frq (yr)	Musth-only	%	Foraging-only	%	Foraging and musth	%
6	-	-	11	11.1	29	30.9
5	-	-	9	9.1	22	23.4
4	2	8.7	9	9.1	14	14.9
3	1	4.3	14	14.1	9	9.6
2	3	13	18	18.2	15	16
1	17	73.9	38	38.4	5	5.3

There were 2732 male-weeks of sightings across the 216 mature males (343 musth and 2394 foraging). 94% of males were more often seen foraging than in musth state. However, the observed proportion (P_o) of 0.125 male-weeks in musth was still significantly higher than the expected proportion (P_e) of 0.106 based on age structure (2-tailed exact binomial test, $p = 0.0015$). 126 males had a ratio below 0.106 while 90 had a greater ratio. There was no significant difference in the age structure of 31 putative residents compared to the whole population ($X^2 = 0.57569$, df = 2, $p = 0.749$), therefore P_e was considered the same for the total population. The total number of male-weeks observed for this subset was 1308, split into 93 musth and 1215 foraging male-weeks respectively. P_o for this subset was 0.071, significantly lower than expected (exact binomial test, $p < 0.0001$).

The sample size for the GLMM was reduced from 216 to 176 after removing the oldest age class (n = 2) and males sighted only once, for whom BSI was undefined (n = 38). There were three candidate models to test the relationship between BSI, male age class and motivational state (Table S1). The model including an interaction between age class and state performed best (ANOVA $p < 0.0001$; Table S1), with results in Table 2. Males following a foraging-only or mixed strategy had similar BSIs whereas those following a musth-only state were split, with the younger age classes showing the lowest BSIs and oldest age class showing the highest of any category (Fig. 3A). Males employing different strategies did not segregate spatially within the observation area (Fig. 3B).

Table 2
– Male BSI: model output from highest performing generalized linear model. Males following the musth-only (m) strategy showed significantly lower BSI values than males using the foraging-only (f) strategy or those doing both (f + m). Male strategy and age class interacted significantly for musth-only (m) at the highest age class, with higher BSI values than other categories.

Fixed Effect	Estimate	SE	t-value	p-value
Intercept	4.452123	0.529418	8.409	< 2e-16*
musth only	-2.103830	0.912723	-2.305	0.0212*
foraging & musth	-0.006498	0.361235	-0.018	0.9856
31–40	0.164912	0.296016	0.557	0.5775
41–50	0.559655	0.513164	1.091	0.2755
musth only:31–40	-0.657094	1.027345	-0.640	0.5224
foraging & musth:31–40	-0.550566	0.453086	-1.215	0.2243
musth only:41–50	2.517846	1.088762	2.313	0.0207*
foraging & musth:41–50	-0.865966	0.618111	-1.401	0.1612

Female PA-use

There were 300 females identified, of which 230 were adults. Of these, 137 were seen consistently throughout the first two years of the study, but seven females known to have died later and were removed from the dataset (n = 130 remaining). 50% of females were re-sighted in each year, while 0.2% percent were not seen again and may represent additional mortality or dispersal events (Fig. 4A). Social community size ranged from 2–22 individuals (Fig. 4B). The largest social communities had the lowest median BSI values (Fig. 5A), suggesting that these large communities have more residential members than smaller communities, but this cannot be statistically evaluated as individuals within communities are non-independent (see below) and community size is a variable with only 16 values. Communities exhibited slight differentiation in observed core areas but considerable spatial overlap overall (Fig. 5B).

The MRQAP showed a significant relationship between the association matrix and the BSI similarity matrix. This shows that social associations predict BSI ($p < 0.001$, Table 3), which as a proxy for PA-use, suggests that females and their close social partners have similar temporal use of the PA. However, the effect was weak ($R^2 = 0.01$), suggesting high individual variation.

Table 3
– Female BSI: model output from multiple regression quadratic assignment procedure (MRQAP). Pairwise female BSI was significantly correlated with the simple ratio index after controlling for the Euclidean distance matrix.

Independent variable	Estimate	Two-tailed P-value
Intercept	0.86	< 0.001
Association matrix	0.43	< 0.001
Spatial matrix	-0.46	0.47
Adjusted $R^2 = 0.01$, Residual SE = 0.18, df = 8382		

Discussion

The scale of space-use by large mammals is mismatched with the scale of PAs, a challenge that is not limited to migratory species or large carnivores (Wikramanayake et al., 2008; Chundawat et al., 2016; Tucker et al., 2018). This is especially true in Asia, where PAs are orders of magnitude smaller than counterparts on other continents (Chowdhury et al., 2022). Because space-use is dictated by life history, we examined how these attributes might affect PA-use among Asian elephants. We found that PA-use strategies vary among individuals of the same sex and even social community within a given population. Observations also suggest nearly all adult males and at least half of adult females (i.e. ~3/4 of the population) may not be long-term residents. We consider these observations in more detail and the issues they raise for the reliance on PAs for accommodating elephants and other wide-ranging taxa on highly-modified landscapes.

Although males use the PA disproportionately when reproductive, 14% use it primarily for foraging, with a significant tendency for younger males to use it exclusively for foraging. Males following this strategy included a residential minority, but close to 90% also disperse at some point (Table 1). Those that use the PA during both states were more likely to be seen across years. The progression of musth stages (Fig. 2) suggests that more males switch from foraging to musth within the PA than vice versa. However, musth-only males behave differently. They tend to enter the study area during the early- or peak-phase and many stay through the late-phase (but never forage). Repeated sightings across years were rarest for musth-only bulls (Table 1), similar to observations from India (Keerthipriya et al., 2020). Interestingly, we observed a shift in strategy with age (Fig. 3A). Most musth-only males aged 20–40 were highly mobile and thus seen often when present (at which time they had low BSIs), but did not return annually (undefined BSIs). In contrast, males > 40 years appear to have settled into a more regular cycle of visitation during musth, evidencing significantly longer (inter-annual) BSIs relative to other classes. Thus, even fully sexually mature males seem to require decades of exploration before finally settling into a recurrent ranging pattern, perhaps through an extended process of contests eventually leading to temporal-partitioning with other similarly-aged males. However, we find no evidence of spatial partitioning suggestive of competitive exclusion among bulls following different strategies.

The mixture of strategies employed by males in this population demonstrates that remaining in a limited area during both motivational states is not a viable option despite the PA's relative safety, availability of forage, and presence of many females. The median birth interval for females in this population is 6 years (de Silva et al., 2013), therefore males must leave the PA eventually due to the scarcity of breeding opportunities. Anecdotally, bulls implicated in human fatalities near the study area (3 individuals) were rarely seen in the PA and all exhibited signs of musth when captured (SdS personal observations). It is possible that some fatal encounters resulted from males ranging into unfamiliar areas during musth-induced range expansion. Nevertheless, there have been fewer than five such incidents during the course of this study. Given that males in this population seem largely transient, the rarity of such encounters is striking.

We expected that female PA-use would be related to social relationships because associations are defined in terms of spatiotemporal co-occurrence. However, the fission-fusion process introduces differences among individuals within the same putative community. We found that members of the same community were not necessarily seen at similar frequencies and that the influence of SRI on BSI was significant but weak. We also found a tendency for individuals from larger communities to have lower BSIs, and given that many were seen across multiple years, these individuals were likely to be more residential to the observation area. Earlier studies of this population found that on average, the number of companions an individual had was negatively correlated with the strength of her ties (de Silva et al., 2011a) and that the fission-fusion process undermines assertion of matriarchal dominance (de Silva et al. 2017). Thus, PA-use reflects some combination of individual decision-making and socially-associated movements. Community members may split up owing to local competition and constraints on group size (Nandini et al., 2018). When individuals compete, dominance hierarchies typically function to mitigate conflicts. Strong hierarchies, such as those observed in African savannah elephants, can mediate priority of access to resources, or even safe zones that are more central to PAs (Wittemyer et al., 2007). Because Asian elephants in this population do not exhibit dominance hierarchies, spatiotemporal avoidance may instead buffer against conflicts (de Silva et al., 2017). Individuals may move to less accessible areas within the PA, or outside it entirely (observed anecdotally), without their social companions.

A recent study in Malaysia suggested that agricultural landscapes might be prime habitats for elephants (de la Torre et al., 2021), while studies in Indonesia and Borneo document the propensity of elephants to exploit "degraded" areas associated with forest edges, often outside PAs (Rood et al., 2010; Evans et al., 2020). Although primary forests are often prioritized for biodiversity conservation (Morales-Hidalgo et al., 2015), elephants may prefer to forage in secondary and regenerating landscapes. But we must be extremely careful in interpreting and generalizing from these studies. First, PAs globally are biased towards steeper, higher terrain (Joppa & Pfaff, 2009). In Southeast Asia, PAs often contain of steep slopes, boxing in elephants when lowland valleys are rapidly converted to other land uses (Wilson et al., 2021). Use of "edge" habitat and agricultural areas may reflect the lack of adequate, low-risk, preferred lowland habitat. Much forest already been lost throughout Asia through conversion to intensive agriculture, contrasting with pre-colonial systems of management (Ellis et al., 2021). Thus many populations remaining today may have no choice but to use human-dominated landscapes, despite associated risks and costs (Goswami et al., 2014; de Silva & Leimgruber, 2019).

Many PAs in South Asia run counter to the trend, being frequently located around rivers and other water bodies, largely to protect their catchment zones, but also seasonally host significant populations of elephants and other wildlife. Their attraction to these PAs likely has to do with the presence of both water and monsoon-mediated forage (e.g. floodplains). Our observation that a substantial fraction of the population is non-residential reiterates the importance of permeability between PAs and wider landscapes. Individual-based studies of how other wildlife actually use PAs as well as in human-dominated landscapes (Kumar et al., 2010; Srinivasaiah et al., 2019), though logistically daunting, would further illuminate how strategies vary in response to anthropogenic changes.

Methods

Study area and population

We observed wild Asian elephants inside Udawalawe National Park in southern Sri Lanka. The park is approximately 308 km^2 and contains two reservoirs resulting from the damming of the Walawe river and a tributary, as well as several smaller water sources, situated in a seasonally dry/deciduous scrubland. The PA is encircled by electric fences, however intentional openings as well as breakages allow the movement of wildlife in and out. The superpopulation of elephants using the habitat is estimated to be 804–1160 individuals with a sex ratio of 1.18 in favor of females, with a high degree of seasonal turnover such that only approximately one third to one half the population is within the PA at any given time (de Silva et al., 2011b). Males were observed from 2010–2015 and females were observed from 2007–2015. Observations were made between 0600h to 1830h on tracks driven along a randomly determined route (de Silva et al., 2011a). Individuals were identified through photographic cataloguing (de Silva et al., 2022).

Quantifying PA-use

We quantified the temporal structure of individual PA-use by calculating the number of days that elapsed between consecutive sightings of a given individual, which we termed the "between-sightings interval" (BSI). It provides a measure of how often an individual is in the study area, while accounting for the impossibility of knowing exactly when they enter and exit the PA. A shorter average BSI can indicate that an individual is remaining close to the study area, while a longer BSI allows for the possibility that it ranges further afield. It may be thought of as complementary to residence time, which cannot be defined from sightings alone. To avoid introducing intervals of artificial length, the average BSI for any individual was only calculated over the first and the last sighting for each individual. This necessarily omitted possible inter-annual variation for individuals observed only within a single year (Figure S1).

Defining age classes and strategies for males

Males were assigned into four coarse age classes based on height and the development of secondary sexual features: 21–30, 31–40, 41–50, 51–60. Physiologically, individuals in all classes are capable of being reproductively active and exhibiting musth (Eisenberg et al., 1971; Jainudeen & Katongole, 1972). Younger sub-adult males and males that transitioned into maturity were excluded from statistical analyses. An individual male's motivational state was categorized as foraging-only (f) if he was never seen exhibiting any signs of musth across the study period, musth-only (m) if he was only seen in the musth condition across the study period, and foraging and musth (f + m) if he was seen in either state at any time during the study. For males observed in musth, we also recorded the stage of musth as early, peak, or late based on physical appearance (Figure S2).

Defining social communities for females

To quantify adult female social relationships, we created a group-by-individual matrix from all observations of adult females and calves between 2007–2015. The full dataset was then filtered to include only adult females that were present in the first two years of the study to allow for the possibility that they were available for observation over the full duration of the study (n = 130). Next, we constructed an association matrix using simple ratio index (SRI) as edge weights in the R package *asnipe* (Farine, 2013; Farine & Whitehead, 2015). SRI is a pairwise index of association that describes the proportion of observations where two individuals were seen together out of all possible observations (Ginsberg & Young, 1992; Whitehead, 2008). An association matrix and corresponding social network were constructed for each of the first two years of the study separately. We then used a Louvain clustering algorithm (package *igraph*, Csardi & Nepusz, 2014) to detect communities within each of the social networks, and used a dynamic community detection algorithm to identify whether social communities were the same between the two years. This algorithm used a reciprocal majority method, i.e., any network clusters that had more than half of the same members between subsequent years were considered the same social community (Liechti & Bonhoeffer 2020). This method allowed us to assign each female to one social community across the entire study period.

Analysis

Statistical analyses were conducted in Microsoft Excel™ and R (R development core team 2019). For males, we tested for preferential use of the study area based on motivational state with a two-sided binomial test, under null expectations based on the proportion of time Asian elephants have been documented to spend in musth within a year relative to the age distribution of the sampled individuals. Individuals aged 21–30 on average are expected to spend 22.5 days (~ 3.21 weeks or 6.18% of the year) in musth, and individuals over 30 are expected to spend on average 45 days (~ 6.49 weeks or 12.48% of the year; Jainudeen & Katongole, 1972). This is equivalent to a proportion of ~ 0.0618 for those aged 21–30 and ~ 0.1248 for those aged > 30. We first checked whether our own observations of musth durations were in agreement with the literature by estimating the duration in days for all age classes > 20 years within our population. We calculated the proportion of sightings for musth vs. non-musth in weeks as opposed to days because sampling did not take place on a daily basis. The unit of measurement is therefore referred to as "male-weeks." Sightings were aggregated by week for each individual and scored as 0 if not seen within that week, 1 if seen only foraging, and 2 if seen in musth at any time during that week. We calculated the expected proportion of musth male-weeks (P_e) as:

$$P_e = 0.0618(N_{21-30}/N_s) + 0.1248(N_{>30}/N_s)$$

where N_s is the total number of individuals within the sample and N_i represents the number of individuals in age class i. We first tested whether there was a significant difference between the expected and observed proportions (P_o) of musth-weeks at the level of the whole population, and then compared this to the subset of possible residents (defined as BSI < 90 days and seen across multiple years) using the exact binomial test with Bonferroni-corrected $\alpha = 0.025$.

To test whether male BSI was influenced by age class or musth state, we constructed a series of generalized linear mixed models (GLMM) using a gaussian logit link function in the R package *lme4* (Bates et al. 2015). For each model, BSI was the dependent variable and the random effects were individual ID, month, and year. The possible covariates, motivational state and age class, were tested for correlation using a Fisher's Exact Test to determine how to structure models, i.e., if age class and state should be included as covariates in models. We evaluated and selected the best fitting model using an analysis of variance test (package *stats*, R Core Team 2021).

To test whether social associations explain similarity in female PA-use, we used a multiple regression quadratic assignment procedure (MRQAP; Dekker et al., 2007; R package *asnipe*). We used three matrices of pairwise metrics to discern the relationship between social association and similarity in BSI while accounting for spatial autocorrelation. First, the dependent variable was a matrix consisting of the pairwise Pearson's correlation coefficient for the average BSI of each female with every other female across all 8 years. The independent variable was the pairwise SRI association matrix, representing the strength of association between individuals. Finally, we accounted for spatial autocorrelation by calculating a pairwise index of spatial use (i.e., the spatial matrix). This was done by calculating a centroid for each female using coordinates from all sightings of that individual. We then calculated Euclidean distances among the centroids of each pair of individuals to represent similarity in their space use. The MRQAP model tests whether the dependent matrix (pairwise correlation in average BSI) is explained by the independent matrix (pairwise association index) while controlling for the non-independence of the covariate matrix (pairwise Euclidean distance).

Declarations

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Author Contributions

SdS conceived of the study; AM, CM, and SdS conducted data analysis and wrote the manuscript. SdS, TVP, and USW, collected the data; UKP and DKW provided research infrastructure and technical input.

Data accessibility

Data will be made available in the Dryad (datadryad.org) repository upon acceptance.

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Figures

Figure 1

Study site. Udawalawe National Park is located in southern Sri Lanka along one of the edges of elephant range in the country (shaded yellow, inset) and contains two reservoirs constructed between 1970 and 2000 as well as smaller water sources. Solid outlines show recognized park boundaries, dashed outlines show edge of elephant range. Area 1 is the observation area with an accessible road network (visible); areas of type 2 represent forested sanctuaries or mixed-use lands of varying designations for which boundaries are not always clear; areas of type 3 represent agriculture and settlement mosaics in which elephants are present; areas of type 4 represent agricultural mosaics with denser settlements where elephants are absent except for occasional incursions by bulls.

Figure 2

Musth expression and strategies. (A) Distribution of male ages across strategies (n=216). The dot size reflects the relative number of males across age classes and musth categories. Grey bars are proportional to the total number of individuals observed in each row or column. Age class and strategy were significantly associated (Fisher's exact test $p < 0.0001$). **(B)** Musth duration by age class. **(C)** Observed musth stages for males that were seen only in musth (n=23), or those seen in both musth and foraging states (n=99).

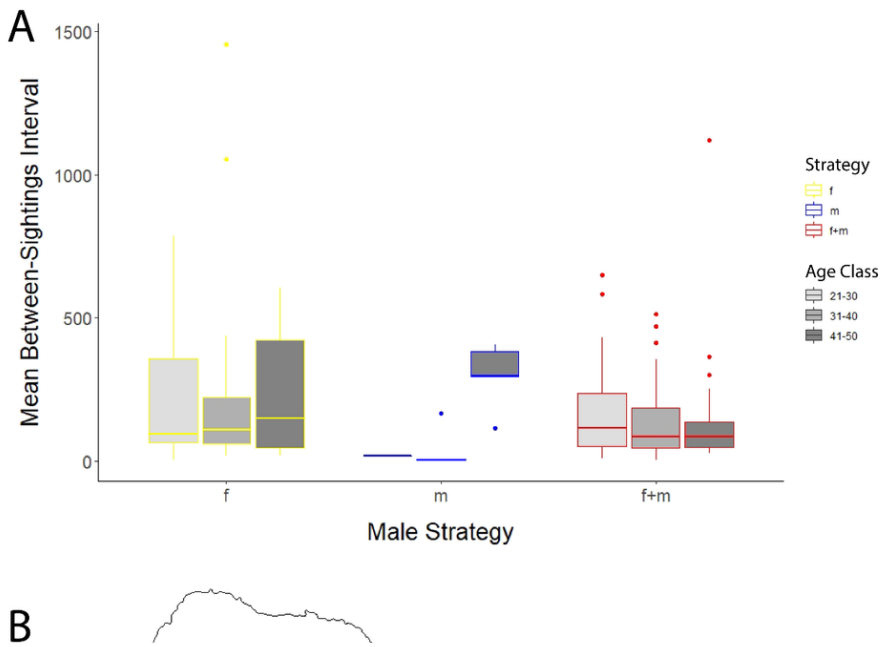

Figure 3

Male PA-use by age and strategy. (A) Average length of between-sightings interval (BSI) by male age and strategy. Males employing the foraging-only strategy tend to have longer BSIs on average than those employing other strategies, while age is not overall an important influence. However, there was an interaction of age and strategy, with BSIs of musth-only males being significantly shorter than those with other strategies. This was driven by males aged 21-40, while BSIs of males in the 41-50 age class were significantly longer (see table 3). **(B)** Space use of males following each of the different strategies, indicated by the same color as (A). Males exhibiting different strategies show no visible spatial differentiation within our central observation area.

Figure 4

Sightings and social affiliations of adult females (n=130). (A) Individuals were required to be seen in both of the first years of the study in order to be included in our sample but half (65 individuals) were seen across all nine. Colors indicate community assignment; individuals from the same community differ in how frequently they were seen. **(B)** Community size and structure.

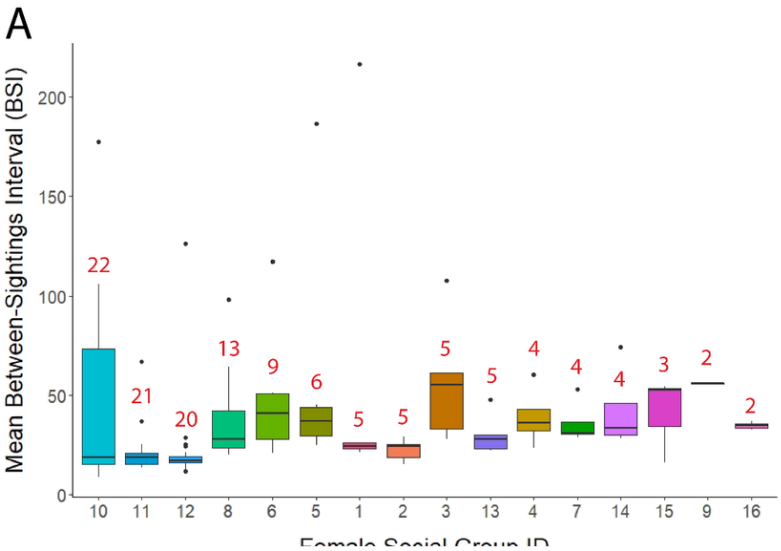

Figure 5

Female BSI and space use. (A) Mean between-sightings-interval (BSI) for adult females when individuals are grouped by social assignment. Numbers along the x-axis correspond to community identity (Figure 4) and are ordered by community size from largest (left, 22 individuals) to smallest (right, 2 individuals). **(B)** Space use for 2 communities with the highest (orange & green, communities 3 & 9) and lowest median BSI (turquoise & blue, communities 10 & 12), demonstrating high spatial overlap between putative residents and non-residents.

Supplementary Files

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- SupplementMalesSciRep20220428.docx