

Short-Term Variation in Sex Ratio Estimates of Asian Elephants Due to Space Use Differences between the Sexes

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Abstract. Selective poaching of males for ivory has led to female-biased adult sex ratios in Asian elephants. Therefore, sex ratio monitoring is common, but is undertaken without examining short-term variability. We examined monthly adult sex ratios during the dry season in Nagarahole and Bandipur National Parks, southern India, using visual capture-recapture and counts of identified males and females. We found monthly differences in sex ratios because males and females used the area differently. Using sightings irrespective of identity gave less female-biased sex ratios during peak summer when censuses are usually carried out. We discuss the implications of our results for management.

Introduction

Anthropogenic disturbances such as poaching and sport hunting have affected population sex ratios in elephants (Poole & Thomsen 1989), ungulates and carnivores (Milner *et al.* 2007). Skewed sex ratios can decrease effective population sizes (Wright 1931; see Allendorf *et al.* 2008) and affect population age structure (Poole & Thomsen 1989; Barnes & Kapela 1991; Milner *et al.* 2007), population viability (Menon *et al.* 1997; Milner-Gulland *et al.* 2003), and reproduction (Ramakrishnan *et al.* 1998; Ishengoma *et al.* 2008). Therefore, sex ratios are considered integral to population monitoring and can be used to make decisions on harvests in game animals (for example, Xie *et al.* 1999) and influence the outcome of population reintroductions (Lambertucci *et al.* 2013). Population sex ratios can also be manipulated through active interventions in order to increase either the effective population size (by introducing males into a population with a female biased sex ratio) or population growth rate (by introducing females into a small population) (Wedekind 2012).

The endangered Asian elephant (*Elephas maximus*) is a species in which poaching for

ivory has led to skewed sex ratios (Menon *et al.* 1997; Ramakrishnan *et al.* 1998), as only males have tusks. There are only ~41,000–52,000 Asian elephants worldwide, of which over half are found in India (Sukumar 2003). Elephant populations in India show varying sex ratios, from 1 adult male : 1.87 adult females (Williams *et al.* 2007) to 1 adult male : 79.6 adult females (Arivazhagan & Sukumar 2005; previously 1 adult male : 101 adult females in the same population, Ramakrishnan *et al.* 1998). The total number of adult male elephants in India was estimated at only 1,500 in 1997 and was thought to be declining further (Menon & Kumar 1998), making sex ratio monitoring imperative.

Moreover, the global monitoring systems set up by CITES, Monitoring the Illegal Killing of Elephants (MIKE) and Elephant Trade Information System (ETIS), are required to assess illegal killing of elephants but carcass data from Asia are limited due to poor reporting rates (Blanc *et al.* 2011) and the difficulty of detecting carcasses in forests. Sex ratios can, therefore, be used along with age structure to better understand poaching offtake (Sukumar *et al.* 1998), make decisions about translocating tuskless adult males to improve sex ratios (Ramakrishnan *et al.* 1998), trace ivory trade routes (Menon *et al.*

1997), and calculate effective population sizes and prioritize populations for conservation.

Despite the need for accurate sex ratio data, systematic study of sex ratios in Asian elephant populations has largely been lacking (but see Arivazhagan & Sukumar 2005). State forest department censuses, conducted over a few days during peak dry season, typically rely on volunteers and forest staff to obtain animal numbers through “total counts” and “block counts” (which incorrectly assume complete detection of all animals in the entire area/blocks sampled) and to obtain age-sex structures through “waterhole counts”, in which elephants are age-sex classified when they visit waterholes (Rangarajan *et al.* 2010). Rangarajan *et al.* (2010) called for a critical scientific evaluation of the methods used to obtain age-sex structures.

Our first objective was, therefore, to find out whether the adult sex ratio obtained over a few days would be representative of the adult sex ratio during the dry season or whether there was short-term variability even within the dry season. Second, sex ratios calculated during “waterhole counts” and even by researchers in the past using line transects, fixed routes, or a population survey, are usually based on the total counts of males and females observed during the study (Karanth & Sunquist 1992; Ramakrishnan *et al.* 1998; Baskaran *et al.* 2010) rather than on the estimated population sizes of males and females. Since individuals are not identified and total counts are used, sex ratios could be biased if there is differential detectability of the sexes. Therefore, our second objective was to find out how adult sex ratios based on total counts of males and females, in the absence of individual identity, compared with 1) sex ratios based on capture-recapture population estimates of the sexes or 2) sex ratios based on counts of identified males and females.

Methods

Study area

The sampling area (~100 km²) was in the dry deciduous forest of Nagarahole National Park

and Tiger Reserve (11.85304°–12.26089°N, 76.00075°–76.27996°E) and in Bandipur National Park and Tiger Reserve (11.59234°–11.94884°N, 76.20850°–76.86904°E) in southern India (Fig. 1). Nagarahole and Bandipur form part of a larger contiguous landscape that holds the largest Asian elephant population (~8500 elephants, Rangarajan *et al.* 2010) in the world. Between Nagarahole and Bandipur lies the Kabini reservoir, the receding backwaters of which support dense congregations of elephants and other herbivores, especially during the dry season (Karanth & Sunquist 1992). Sampling was carried out both in the forest and in the open areas around the backwaters in Nagarahole and along the backwaters in Bandipur.

Field methods

The field study was non-invasive in nature and field permits were obtained from the Karnataka State Forest Department. We drove along pre-selected routes in the study area (~40 km per day) and collected data on elephants. The study area has a good forest road network (Goswami *et al.* 2007) and elephants are used to tourist vehicles, allowing for maximal encounter probabilities. Elephants were aged, sexed, and identified based on a combination of ear, tail, body, and tusk/tush characteristics (Vidya *et al.* 2014). Animals were broadly age-classified as calves, juveniles, sub-adults, and adults (≥ 15 years old) (Vidya *et al.* 2014). The demography data for this study was obtained from 689 sightings of animals over 84

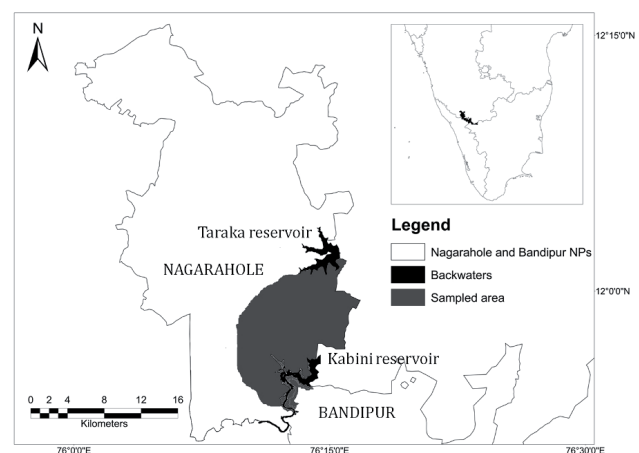


Figure 1. Map of the study area with the rough area sampled and inset of the location of the study area in southern India.

days (Table 1), with roughly equal sampling effort from ~7 am – 6 pm, between March-June 2009. These sightings comprised 2900 individuals, of which 1286 were adults (986 females and 300 males, including re-sightings of the same individuals). The present study was limited to the dry season as were previous censuses and research studies because of the logistics of sampling and low encounter rates during the monsoons.

Data analysis

In order to find out whether sex ratios based on short sampling periods were representative of sex ratio across the dry season, we calculated sex ratios based on about a week's sampling (henceforth, referred to as 'one-week-per-month') and about a month's (henceforth, referred to as 'entire month') sampling, during each month for four months. The one-week-per-month sampling was carried out between the 8th and 17th of each month (exact dates provided in Table 1). In order to address the second objective of comparing sex ratios obtained with and without individual identity, we obtained sex ratios from 1) total encounters of adult males and females during the sampling period, 2) counts of identified adult males and females, 3) capture-recapture estimates of adult male and adult female population sizes (see paragraph below).

Elephants were individually identified based on natural physical characteristics (Vidya *et al.* 2014). We used standard capture-recapture methods (Seber 1982; Williams *et al.* 2002) to estimate male and female population sizes. Multiple sightings (or captures) over a day were consolidated into one occasion (*sensu* Williams *et al.* 2002) per day. The resulting dataset

contained 84 occasions (Table 1). The subset of data between the 8th and 17th of each month comprised 31 occasions.

Capture histories were constructed for identified adults, separately for each dataset, and analyzed using the program MARK (White & Burnham 1999). The assumptions of equal catchability and survival across individuals were tested using standard tests (TEST2 and TEST3) in program RELEASE (Burnham *et al.* 1987) from within MARK. The assumptions of equal survival and detection were met by the datasets of males. The assumption of equal survival across individuals was met by the one-week-per-month but not the entire month dataset of females, and both female datasets showed detection heterogeneity. This heterogeneity in female detection and survival (which comes from differences in emigration, which is treated in the test as part of survival) were probably due to the absence of geographic closure as the study area is part of a larger continuous forested landscape. Therefore, the Robust Design model (Kendall & Nichols 1995; Kendall *et al.* 1995, 1997) and POPAN formulation of the Jolly-Seber class of models (Schwarz & Arnason 1996) that do not assume geographic closure were used to estimate population parameters.

The Robust Design model involves sampling primary occasions, which are widely spaced and allow for migration, births and deaths, and secondary occasions (within each primary occasion), across which the population is effectively closed. In our analysis, the period between 8th and 17th of March, April, May and June, 2009 formed the four primary occasions of approximately equal sampling effort. Secondary occasions were days within the primary

Table 1. Sampling effort in different months during the dry season of 2009 in Nagarhole National Park and Bandipur Tiger Reserve, number of adult elephants sighted during the one-week-per-month and entire month datasets, and secondary occasions (SO) for the Robust Design analysis.

Month	# days	Entire month		One-week-per-month		Robust design analysis data	
		Total # adults	# unique adults	Total # adults	# unique adults	SO within each primary occasion (dates)	# SO (days)
March	18	212	63	95	43	8, 10, 12, 13, 14, 16, 17	7
April	19	327	108	136	60	9, 10, 11, 13,14,15,16,17	8
May	25	364	125	152	73	8, 9, 11, 12, 13,14,15,16,17	9
June	22	384	94	136	60	8, 9, 12, 13, 14, 15, 17	7

occasions and, since they were closely spaced, the closure assumption seemed to be valid for secondary occasions (Kendall & Nichols 1995). Population size for each primary occasion was estimated based on the model with the lowest AICc value. POPAN postulates the existence of a superpopulation (N^*), from which new entrants can immigrate to the study area. Therefore, in addition to recapture rates and the survival rates (also estimated in Robust Design), this model has the parameters $b/pent$ (probability of entry). The POPAN analysis was performed using both the entire month's sampling and sampling between only the 8th and 17th of each month. Superpopulation estimates from the model with the lowest AICc value were used for further analyses. Sex ratios were calculated from estimates of population size obtained from the above methods and error terms for these sex ratios calculated using the method of propagation of errors. The error, ΔR , for any ratio, A/B , is given by the following relationship,

$$\Delta R = \frac{A}{B} \sqrt{\left(\frac{\Delta A}{A}\right)^2 + \left(\frac{\Delta B}{B}\right)^2}$$

where ΔA and ΔB are the error terms for random variables, A and B , respectively (Birge 1939). Statistical analyses were carried out using Statistica 5 (StatSoft, Inc. 1996).

Results

Sex ratios based on unique individuals sighted

The total numbers of unique adult females and adult males seen during the one-week-per-month

dataset were 109 and 25, respectively, and during the entire month dataset, 153 and 31, respectively, giving rise to sex ratios of 1:4.4 (adult males : adult females) and 1:4.9 overall based on these two datasets. Sex ratios varied across months, from 1:2.9 to 1:4.8 based on the one-week-per-month dataset (Fig. 2a) and even more, from 1:2.9 to 1:5.6, based on the entire month dataset (Fig. 2b). Changes across months were consistent with the cumulative counts of males plateauing quickly compared to those of females (Fig. 3).

Robust Design

The Robust Design analysis of data on adult females yielded a model with constant survival probability, time-varying probabilities of capture and recapture set equal to each other, and movement constrained to be Markovian as the best model (Table 2). Setting capture and recapture probabilities to be equal meant that the probability of sighting an elephant was not dependent on its earlier sighting history. Estimates from this best model showed considerable monthly changes in adult female population size (Table 3).

The best model for adult males was different from the best model for females, and had capture and recapture probabilities constrained to be constant over secondary occasions, with Markovian movement and constant survival (Table 2). Based on the Robust Design, using data from one-week-per-month as the primary occasions, sex ratios were found to vary from 1:2.9 to 1:4.7 across months (Fig. 2a).

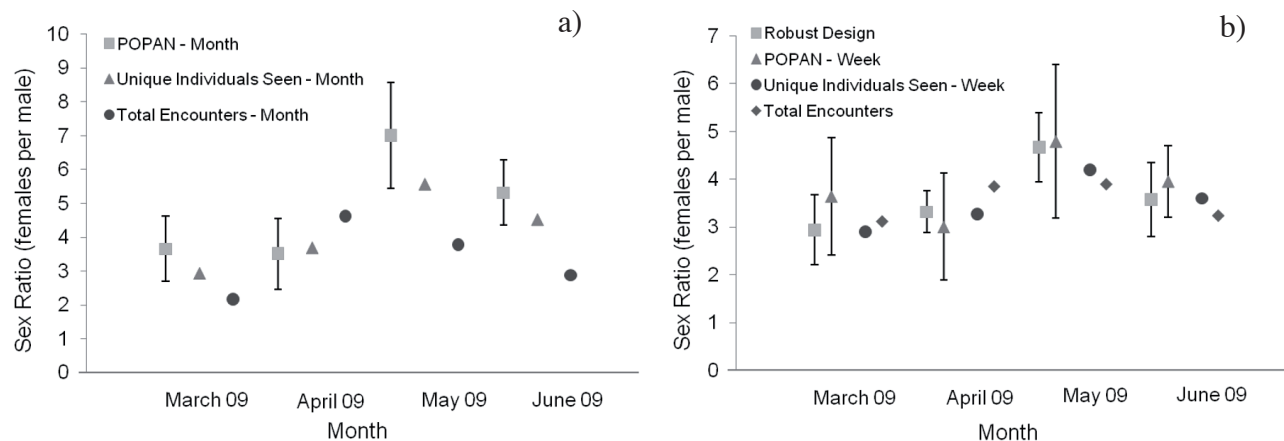


Figure 2. Monthly adult sex ratios (number of adult females per adult male) and 95% CIs calculated using different methods, based on data from a) one-week-per-month and b) the entire month.

Table 2. Results from Robust Design models for adult females and adult males. The model likelihoods, AICc, number of parameters, and deviance for various models are shown. The different models are ranked according to the AICc values calculated based on the combination of the likelihood of the model and the number of parameters: p : probability of initial capture, c : probability of recapture, s : survival; N : population size in the study area; (t): different estimate for each occasion, (.): constant estimate, (month): different estimate for each month. Movement can be modelled as null, random, or Markovian.

Sex	Model	AICc	Delta AICc	AICc Weight	Model Lik.	Num Par	Deviance
Females	s(.), p(t)=c(t), Markovian, N(Month)	743.083	0.000	0.914	1.000	37.0	860.621
	s(.), p(t)=c(t), Random, N(Month)	747.807	4.724	0.086	0.094	38.0	862.886
	s(.), p(t)=c(t), Null, N(Month)	769.901	26.819	0.000	0.000	35.0	892.314
	s(.), p(Month)=c(Month), Markovian, N(Month)	846.992	103.910	0.000	0.000	12.0	1021.733
	s(.), p(Month)=c(Month), Random, N(Month)	849.264	106.181	0.000	0.000	12.0	1024.004
	s(.), p(.)=c(.), Markovian, N(Month)	850.611	107.528	0.000	0.000	9.0	1031.707
	s(.), p(.)=c(.), Random, N(Month)	852.878	109.795	0	0	9	1033.974
	s(.), p(Month)=c(Month), Null, N(Month)	867.939	124.856	0	0	9	1049.035
	s(.), p(.)=c(.), Null, N(Month)	883.607	140.525	0	0	9	1064.704
Males	s(.), p(.)=c(.), Markovian, N(Month)	384.562	0.000	0.601	1.000	9.0	390.306
	s(.), p(.)=c(.), Random, N(Month)	385.897	1.336	0.308	0.513	9.0	391.642
	s(.), p(Month)=c(Month), Random, N(Month)	389.541	4.979	0.050	0.083	12.0	387.927
	s(.), p(.)=c(.), Null, N(Month)	390.915	6.354	0.025	0.042	9.0	396.660
	s(.), p(Month)=c(Month), Null, N(Month)	393.114	8.552	0.008	0.014	12.0	391.500
	s(.), p(Month)=c(Month), Markovian, N(Month)	393.114	8.552	0.008	0.014	12.0	391.500
	s(.), p(t)=c(t), Null, N(Month)	417.102	32.540	0	0	34	344.450
	s(.), p(t)=c(t), Markovian, N(Month)	419.901	35.339	0	0	36	338.779
	s(.), p(t)=c(t), Random, N(Month)	425.385	40.823	0	0	37	339.860

POPAN

The best model based on POPAN analysis also varied between adult females and males. The best model for adult males had constant survival, constant probability of entry, and constant

capture probability based on both the one-week-per-month and entire month datasets. The best model for adult females for the one-week-per-month datasets for April and May had constant survival, constant probability of entry, and time-varying capture probabilities, the best model

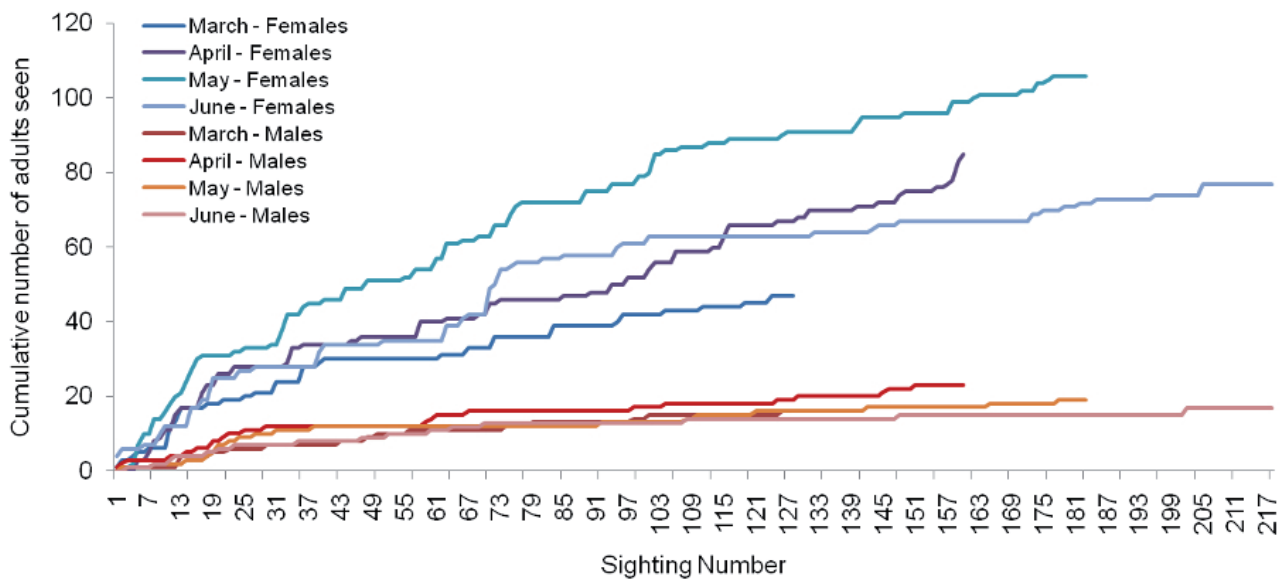


Figure 3. Cumulative counts of uniquely identified females and males in different months.

Table 3. Population size estimates (N) obtained from the respective Robust Design models with the lowest AICc for adult females and males.

Month	N	SE	Lower 95% CI	Upper 95% CI
Females				
Mar 09	35.030	2.409	32.769	43.944
Apr 09	49.058	2.276	46.832	57.236
May 09	67.201	3.939	62.358	79.032
Jun 09	50.684	2.580	48.068	59.707
Males				
Mar 09	11.904	1.272	11.117	18.007
Apr 09	14.764	0.726	14.158	17.681
May 09	14.386	0.768	14.032	18.606
Jun 09	14.170	1.386	13.186	20.336

for March had constant survival and capture probabilities, but time-varying probability of entry, and the best model for June had time-varying survival and capture probabilities, but constant probability of entry. The best models for the entire month dataset for March, May, and June showed constant survival and probability of entry but time-varying capture probabilities. The best model for the entire month data from April had constant survival but time-varying capture and entry probabilities. The sex ratios from the best model estimates (Tables 4 & 5) varied across months from 1:3 to 1:4.8 based on the one-week-per-month dataset (Fig. 2a) and from 1:3.5 to 1:7 based on the entire month dataset (Fig. 2b).

Table 4. Estimates of superpopulation size (N) from POPAN run with data from the one-week-per-month dataset (see Table 1) for each month for adult females and adult males. Superpopulation size estimates are expected to be larger than Robust Design population size estimates.

Intervals	N	SE	Lower 95% CI	Upper 95% CI
Females				
Mar 09	42.591	5.162	36.285	58.175
Apr 09	53.775	4.034	48.986	66.243
May 09	80.604	6.648	70.982	97.954
Jun 09	52.024	3.140	48.630	62.483
Males				
Mar 09	11.670	1.422	11.052	19.666
Apr 09	17.864	3.120	14.963	29.495
May 09	16.799	2.512	14.621	26.627
Jun 09	13.128	0.988	13.002	19.789

Table 5. Estimates of superpopulation size (N) from POPAN run with the entire month datasets of adult females and adult males.

Intervals	N	SE	Lower 95% CI	Upper 95% CI
Females				
Mar 09	63.741	5.931	55.532	79.847
Apr 09	105.000	7.463	94.856	125.585
May 09	147.211	10.144	131.619	172.293
Jun 09	94.704	5.569	86.697	109.324
Males				
Mar 09	17.403	1.667	16.223	24.823
Apr 09	29.816	3.972	25.362	42.671
May 09	20.960	1.894	19.399	28.625
Jun 09	17.787	1.267	17.086	24.215

Total encounters and a comparison of sex ratios

The overall sex ratio (across months combined) calculated using the total numbers of males and females encountered irrespective of individual identity was 1:3.3, as opposed to 1:4.9 based on the unique individuals sighted (see first Results paragraph). The sex ratios from total encounters were somewhat less variable over months than those calculated using other methods (Fig. 2), and varied from 1:3.1 to 1:3.9 based on the one-week-per-month dataset, and from 1:2.2 to 1:4.6 based on the entire month dataset. In May and June, total encounters gave less female-biased sex ratios than the other methods.

When sex ratios were compared across the four months, there was a significant effect of month for the one-week-per-month dataset based on the four different methods (Repeated measures ANOVA: $F_{3,9} = 8.835$, $P = 0.005$), as well as the entire month dataset based on only POPAN and number of unique individuals (Repeated measures ANOVA: $F_{3,3} = 17.039$, $P = 0.022$), as total encounters were not so variable. Post-hoc tests showed significant differences in sex ratios between March and May, and April and May (Tukey's HSD tests, $P < 0.05$) based on both the one-week-per-month and entire month datasets. We also found a significant difference between the sex ratios based on the one-week-per-month dataset and the entire month dataset (Paired t test using sex ratios from POPAN and the number of unique individuals, matched for the month, $t_7 =$

-3.152, $P = 0.016$), with the sex ratio being less female-biased based on the shorter time period of sampling (mean_{week} = 1:3.68, mean_{month} = 1:4.53).

Discussion

Sex ratios across time

In sexually dimorphic polygynous species, the adult sex ratio is seldom 1:1 because of increased mortality in males (Promislow 1992). The “natural” adult sex ratio of undisturbed populations of Asian elephants is possibly ~1:2 (males : females) (McKay 1973; Williams *et al.* 2007). Therefore, adult sex ratios in our study area were abnormally skewed, possibly because of historical poaching. We show for the first time that there was considerable variability in adult sex ratios even within months across the dry season. Therefore, sex ratios from annual or biennial censuses of 2–3 days may not be meaningful as they can differ depending on when the census was undertaken (see Figure 4). While the broader-scale adult sex ratio (from census data of Karnataka) was estimated at 1:3.7 in 2002 (Sukumar *et al.* 2002) and 1:2.2 in 2010 (Baskaran & Sukumar 2011), whether this change reflects actually improved sex ratio or local sampling issues is difficult to disentangle. We found monthly sex ratios varying from 1:2.9 to 1:5.6 (based on the number of unique individuals seen) or from 1:3.5 to 1:7.0 (based on POPAN). Doubling of sex ratios in this range of values is disconcerting because short-term estimates of sex ratio may then reach opposite conclusions about the long-term status of males in the population. This is especially a problem in populations with sex ratios that are not very skewed because small changes in sex ratio arise from large changes in actual numbers of one sex (while the opposite is true if the sex ratio is already very skewed), making the estimation of sex ratios more crucial in such populations.

Our overall sex ratio estimate from counts of identified adults was 1:4.9 (M:F), while adult sex ratios in previous studies in roughly the same study area and carried out by researchers using technically correct methods were 1:3.1 (Vidya *et al.* 2003), 1:5.8 (Arivazhagan & Sukumar

2005), and 1:4.3 (Goswami *et al.* 2007). The adult sex ratio based on the Forest Department census in Nagarahole and Bandipur combined was 1:3.6 in 2002 and 1:2.5 in 2010 (Nagarahole separately: 1:2.7 in 2002 and 1:2.1 in 2010, Bandipur separately: 1:4.5 in 2002 and 1:2.7 in 2010; Sukumar *et al.* 2002; Baskaran & Sukumar 2011). When faced with such data from different time points, it is tempting to read a pattern into it across years and make inferences about poaching. Managers may be forced to make decisions regarding patrolling and stepping up of anti-poaching efforts based on such “changes” in sex ratio, from, say, 1:3.1 to 1:5.8, which would indeed be a drastic change if these sex ratios were correct. However, since we find that short-term temporal variation over the course of months can be of the same range, it is not possible to infer patterns about long-term variation in sex ratios from the previous studies in this area. We found that over 60 days of data were required to obtain a plateauing of sex ratios (Fig. 4), although this time period may depend on when the study is started, suggesting that short-term censuses may not be reliable.

It is interesting that the short-term differences in sex ratios were brought about by sex-specific differences in space use, as evidenced by the different best models obtained from Robust Design and POPAN analyses, by adult females and males. In both analyses, the best models for females included variable capture probabilities across time, while those for males included constant capture probabilities. We found, based on field observations also, that many females entered the study area during the peak of the dry season (April-May), while there was no correspondingly high increase in the number of males (the number of unique females rose from 47 in March to 106 in May, while the number of unique males was 16 in March and 19 in May). Thus, differences in movement patterns/use of the study area caused temporal changes in sex ratios. Apart from management relevance, such variability could also be biologically significant as it can affect mating opportunities. For instance, if the proportion of females coming into oestrous remains constant across months, a larger number of available females in certain months

could increase mating opportunities for males. In general, operational sex ratios are expected to and have been found to influence various aspects of mating behaviour (Emlen & Oring 1977; see Weir *et al.* 2011 and references therein).

Sex ratios using unidentified versus identified individuals

Differences in the detectability of males and females can bias sex ratios if the total counts of females and males are used. The accuracy of such a sex ratio estimate is, therefore, likely to depend on what proportion of males and females in the population have been sampled and the true population sex ratio. While the sex ratios based on total counts were less variable across months, they were also less female-biased than sex ratios from other methods during the peak dry season, when censuses are usually carried out. This is possibly why census data tend to show less skewed adult sex ratios than longer term studies (see data in previous section). The difference in sex ratio estimates between using identified individuals and total encounters (irrespective of identity) may also be one of behaviour. Male and female elephants can respond very differently to habitats and humans (Sukumar & Gadgil 1988; Evans & Harris 2012). In our study area, we found that males remained in open areas more

often than females, making repeat sightings of them more probable (average numbers of repeat sightings for males and females in open areas were 9.6 and 6.6, respectively). On the other hand, inside denser forests, adult males could be more difficult to sight because of being solitary and, possibly, even more elusive. Therefore, sex ratios in the absence of individual identification can be misleading.

Overall implications

Apart from implications for management, short-term variations in sex ratios can have significant implications for animals in terms of possibilities for interaction and mating opportunities. The extent to which mating opportunities are affected would depend on oestrous synchrony and dominance hierarchies amongst males that affect monopolizability of females. One might argue that if sex ratio differences across months occur in a study area that is a few to several hundred square kilometres in size (a Protected Area in India, such as in our study), coordinated censuses at a larger scale might recover correct sex ratios even if carried out for a short time. However, when sex ratios are calculated using total counts, as they are during large-scale censuses, they can be quite different from the real sex ratios. We also estimated sex ratios from the

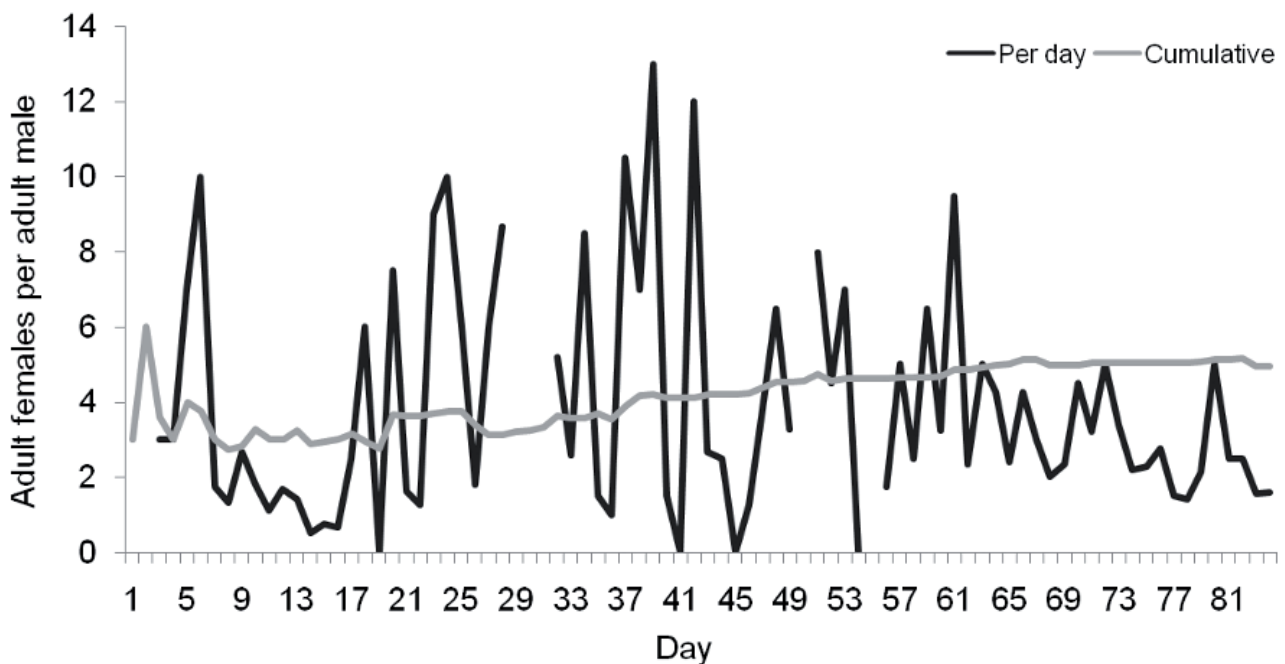


Figure 4. Daily adult sex ratio and cumulative sex ratios based on individually identified animals across the sampled days. The dashed line indicates the final sex ratio obtained (1 male : 4.9 females).

simple Lincoln-Petersen method of estimating population sizes, which can be calculated by local managers, but found the estimates to be too crude to be useful (data not shown). While short-term censuses provide estimates of numbers of animals in an area, which are important in affecting density-dependent processes, long-term studies on identified individuals that provide data on population numbers (that are similar to those from capture-recapture sampling), but additionally provide a wealth of information on other aspects of the species (Clutton-Brock & Sheldon 2010) may be the way forward in monitoring large mammal populations. However, since wildlife protection departments rarely have the time or expertise to carry out long-term, individual-based monitoring of populations, it might help if competent researchers obtain such data from at least select populations of elephants in high density areas (Rangarajan *et al.* 2010; it would be impractical to obtain detailed data from the entire 12,000 km² landscape). In the context of male poaching, it might be worth monitoring at least identified adult males (Goswami *et al.* 2007) rather than relying on census data or carcasses (which are very difficult to find in Asian forests). Another reason for monitoring individual males is that pubertal males disperse not just from their natal herds, but also from their natal home ranges to different locations (locational dispersal; Vidya & Sukumar 2005; Vidya *et al.* 2005). Therefore, individual turnover in an area due to dispersals could give rise to the same counts. Locational dispersal of males also implies that poaching young males can affect areas that those males would otherwise disperse to, even if there was adequate protection in those areas. If waterhole counts are undertaken, it would be important to obtain photographs so that an attempt can be made at identifying individuals rather than using total counts.

Acknowledgments

This work was supported by the Department of Science and Technology's (Government of India) Ramanujan Fellowship (to TNCV), Council of Scientific and Industrial Research, Government of India (Grant No.37(1375)/09/EMR-II), National Geographic Society, USA (Grant No. 8719-09),

and JNCASR. MG was supported by JNCASR's Integrated Ph.D. programme in Evolutionary and Organismal Biology and SR was supported by JNCASR's SRFP programme. We thank the office of the PCCF, Karnataka Forest Department, for field permits, and various officials, from the PCCF to the Range Forest Officers, as well as the staff of Nagarhole and Bandipur National Parks, for permits and support at the field site. We thank Arjun Ghosh and Ashok Kumar for help with data collection and Mr. Gunda, Mr. Rajesh, Mr. Binu, and Mr. Althaf for field assistance. We thank Devcharan Jathanna, Centre for Wildlife Studies, Bangalore, for useful advice on data analysis. We thank Hansraj Gautam for help with GIS. We also thank two anonymous reviewers for providing useful comments on a previous version of our paper.

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