A Simulation Study of Bias in Two Standard Mark-Recapture Estimators when used on Populations with Differing Social Structures under Different Trapping Scenarios

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by

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CERTIFICATE

This is to certify that the work embodied in this thesis entitled "**A simulation study of bias in two standard mark-recapture estimators when used on populations with differing social structures under different trapping scenarios**" has been carried out by Mr. Manan Gupta under our supervision at the Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced Scientific Research, Bengaluru, India, and that the results in this thesis have not previously formed the basis for the award of any other diploma, degree or fellowship.

Date: March 31, 2015 Dr. T. N. C. Vidya Prof. Amitabh Joshi

DECLARATION

I declare that the matter presented in my thesis entitled "**A simulation study of bias in two standard mark-recapture estimators when used on populations with differing social structures under different trapping scenarios** " is the result of studies carried out by me at the Evolutionary and Organismal Biology Unit of the Jawaharlal Nehru Centre for Advanced Scientific Research, Bangalore, India, under the supervision of Dr. T. N. C. Vidya and Prof. Amitabh Joshi, and that this work has not been submitted elsewhere for any other degree.

In keeping with the general practice of reporting scientific observations, due acknowledgement has been made wherever the work described has been based on the findings of other investigators. Any omission, which might occur by oversight or error of judgment, is regretted.

Place: Bangalore Manan Gupta

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CHAPTER 1: INTRODUCTION

The estimation of population size is important in studying population dynamics (Kingsland 1995, Turchin 2003), in calculating effective population sizes in studies of evolutionary dynamics (Nunney and Elam 1994, Frankham 1995), in estimating the sex-ratio of populations (Clutton-Brock 1986, Clutton-Brock and Iason 1986), and in monitoring the status of populations which are at risk of extinction (Jones *et al*. 2013). The estimation of population size in the wild can be challenging as animals may range over vast, inaccessible areas and individuals may not be easily detectable. Social species may present an additional challenge as individuals belonging to different social groups may have varying detectability (Cubaynes *et al*. 2010), especially if these groups have changing compositions over short time periods. While capture-recapture models have been widely used, and progressively refined, in order to estimate the population sizes of animals in the wild (Seber 1982, Williams *et al*. 2002, Amstrup *et al*. 2005), these models do not explicitly consider sociality as a factor that can affect population estimates. Therefore, in this thesis, I examine whether the current statistical methods of population size estimation give unbiased estimates for populations exhibiting different kinds of social structures. Using individual-based simulations, I also explore the effect of population densities, trap densities (sampling intensity), sampling scale, and trap spatial arrangement or distribution on the efficacy of two commonly used mark-recapture estimators, POPAN and Robust Design with heterogeneity.

1.1 Population size estimation

1.1.1 History of population size estimation

Swanson and Stephen (2004) note that the first ever census was conducted in Babylon around 3800 B.C. for taxation purposes. However, as with most of the earliest censuses, the counts were limited to heads of households, males who could be drafted into the military, and taxpayers (Bryan 2004). The first ever complete census might have been conducted by Cecrops, the first king of Athens (Missiakoulis 2010). Cecrops ordered all his citizens to leave a stone each in a predetermined location and the stones in the final heap were then counted out to be around 20,000. The Greek word ΛΑΟΣ (laos) meaning everyone of all age classes is, thus, derived from ΛΑΑΣ (laas) meaning stone (Stageritis 1815, as cited in Missiakoulis 2010). However, since it is logistically not possible to count every individual in most human or animal populations, population size (N) has long been estimated by performing partial counts (C) of the study population and dividing this partial count by the capture probability or probability of detection (β) of an individual present in the study area. Such ratios of partial counts to capture probabilities were used in the early 1600s to estimate population sizes of cities and countries. In examining the effects of the plague of the early 1600s on the London demographics, Graunt (1939) calculated the population size using the per capita death rate and the total number of burials (Hald 1990). In 1802, the French mathematician, Pierre-Simon Laplace calculated the population size of France by dividing the total number of births in France during the previous year by the per capita birth rate. This birth rate was obtained not through a complete census of the population but by censusing a few selected administrative districts called communes for which the birth record was complete and the total population was countable (Cochran 1978, Stigler 1986).

If only part of the study population is sampled (with α being the fraction sampled), the estimated population size $\hat{N}$ is given by

$$\hat{N} = \frac{C}{\hat{\alpha}\hat{\beta}},$$

where $\hat{\alpha}$ and $\hat{\beta}$ are the estimates of fraction of study area sampled and probability of detection of an individual, respectively, and C is the number of total unique individuals sighted or captured (notation following Williams *et al.* (2002)). The estimate for the fraction of area sampled is usually well known in a field study, but the probability of detection cannot be estimated without using more than one capture occasion.

The estimation of animal population sizes received early attention largely in the context of assessment of fish stocks and game animals (Petersen 1889, 1894, Lincoln 1930). Petersen (1889) first used the recapture of marked animals to study the growth and migration of a fish population. He also derived estimates of mortality for that population (Petersen 1894). Lincoln (1930) first used the recapture of marked animals to estimate the total population size of a free-ranging animal population, by what is now referred to as the Lincoln-Petersen estimator (Seber 1982). In the framework of the Lincoln-Petersen estimator, animals are captured on the first occasion, marked for subsequent identification and then released back into the study area. Another set of animals is captured on the second occasion and the numbers of marked and unmarked animals counted. Then, the proportion of marked individuals in the second sample gives an estimate for the probability of detection and can be used in formulating the estimator of population size. Thus, estimated population size is,

$$\widehat{N} = \frac{n_1}{\hat{\beta}};\ \hat{\beta} = \frac{m_2}{n_2};\ \widehat{N} = \frac{n_1 n_2}{m_2}$$

where n_1 is the number of animals captured on the first occasion, n_2 is the number of animals captured on the second occasion and m_2 is the number of marked animals captured on the second occasion. Though Petersen (1889) did mark and release animals in his study, he did not use those data to determine population size, but restricted himself to the estimation of mortality rates (Bailey 1952, Le Cren 1965). Thus, it is generally agreed that Lincoln (1930) was the first to use a capture-mark-recapture method to estimate population size of a wild population. The Lincoln-Petersen estimator assumes that the population is closed to additions, i.e., births and immigrations, over the course of the two sample occasions. It also assumes that all individuals have an equal probability of detection and that no marks are lost or overlooked. The first two assumptions are important to obtain unbiased and precise estimates, but are violated quite often in field studies (Williams *et al.* 2002). Thus, it became necessary to develop models that could estimate capture probabilities over intervals during which a population was open to additions, as well as models that could incorporate capture probabilities that varied over time and amongst individuals. Over the years, increasingly sophisticated methods of estimating population size have been developed that use more than two capture occasions and, therefore, yield more precise estimates for both closed and open populations. These include: (i) closed population models discussed in Otis *et al.* (1978), (ii) the Jolly-Seber and related open population models (Jolly 1965, Seber 1965, Schwarz and Arnason 1996), that are a continuation of earlier work by Darroch (1959), and (iii) the Robust Design models (Pollock 1981, 1982, Kendall and Pollock 1992, Kendall *et al.* 1995, Kendall *et al.* 1997), that incorporate a hierarchical sampling approach with several sets of capture occasions, which are closed to migratory and demographic changes, but across which the population may be open to migration. In addition to these, more recently, new models have been proposed that deal with individual heterogeneity in capture probabilities due to the spatial distribution of individuals with respect to the trap distribution, due to differing physiological states among individuals due to effects of differing capture locations, etc., in much better ways. These include (i) the multistate models (Arnason 1972, 1973, Brownie *et al.* 1993, Schwarz *et al.* 1993) that incorporate the movement of individuals between different areas (states), and (ii) the spatially-explicit capture recapture models (Efford 2004, Borchers and Efford 2008, Royle *et al.* 2009a,b, Borchers 2012). All the models listed above are described in the following sections.

1.1.2 Cormack-Jolly-Seber and Jolly-Seber Models

Darroch (1958) developed estimators for the estimation of population size in the case of multiple capture occasions for a closed population. He also dealt with multiple captures for partially open populations, i.e., he considered the cases of only gains or only losses of individuals but not both, in a subsequent study (Darroch 1959). This directly led to the development of the Cormack-Jolly-Seber (CJS) and Jolly-Seber (JS) open population models (Cormack 1964, Jolly 1965, Seber 1965). The CJS model has two sets of parameters, the survival probabilities (φ_i) and the capture probabilities (p_i), where i denotes the capture occasion. For a particular sequence of capture occasions, a capture history can be created for each individual. A capture history is a string of binary digits of length K (number of capture occasions) with 1's denoting capture and 0's denoting no capture in each capture occasion. Therefore, the likelihood of a particular capture history of 3 occasions, say 110, is given by

$$\Pr(110|released\ on\ occasion\ 1) = \varphi_1 p_2 (1 - \varphi_2 p_3).$$

The likelihoods for the other three capture histories in which the individual was released on the first occasion are shown in Table 1. Likelihoods for all individuals can be multiplied to obtain the complete likelihood for the dataset under the CJS model. The maximum likelihood (ML) estimation approach can be used to obtain estimates for survival and capture probabilities (Amstrup *et al*. 2005). The CJS model makes the following assumptions (Table 2, Seber 1982, Williams *et al*. 2002):

1. All marked animals present in the study area at a given occasion have the same capture probability, p_i.
2. All marked animals present in the study area after capture occasion i have the same survival probability, φ_i.
3. The sampling at each sampling period and release of captured animals are instantaneous (which cannot be met in reality).

4. Any emigration from the study area is permanent.
5. The survival and capture of animals are independent of each other.
6. There is no error in identifying marks and marks are not lost or overlooked.

Table 1 : CJS likelihoods for capture probabilities given first release on occasion 1.

Capture History	Probability
100	$\varphi_1(1-p_2)(1-\varphi_2 p_3)+(1-\varphi_1)$
101	$\varphi_1(1-p_2)\varphi_2 p_3$
110	$\varphi_1 p_2(1-\varphi_2 p_3)$
111	$\varphi_1 p_2 \varphi_2 p_3$

The CJS model (Cormack 1964, Jolly 1965, Seber 1965) did not allow for the estimation of population size. Jolly (1965) and Seber (1965) also developed approaches that allowed for estimation of population size (*N*) and recruitment (*B*), and the resulting models came to be known as the Jolly-Seber open population models. The Jolly-Seber approach uses unconditional likelihoods of capture histories as opposed to the conditional likelihoods used in the CJS models. These models have number of births or entrants, B_i, as a derived parameter which never enters the likelihood function. Thus, it is impossible to constrain B_i to always be greater than or equal to 0. For similar reasons, it is impossible to have a death only model ($B_i = 0$) or a model where births are equal across groups ($B_i = B$ for all i) unlike in the framework of Lebreton *et al.* (1992).

1.1.3 POPAN

An alternative formulation of the Jolly-Seber models is POPAN (Schwarz and Arnason 1996), which assumes a superpopulation. The superpopulation is defined as all the individuals that have a non-zero probability of capture during the entire duration of the study period, i.e.,

$$N = \sum_{i=0}^{K-1} B_i,$$

where N is the superpopulation size, K is the number of capture occasions and B_i are the number of additions after interval i with B_0 being the initial number of individuals present in the study area. The removals are taken into account in the survival probabilities (φ_i), thus, it is known as apparent survival and not actual survival. The probability of entrance (b_i) is the probability that an individual will enter the study area from the hypothetical study area such that $E[B_i] = Nb_i$. This mean that $b_0 + b_1 + \cdots + b_{K-1} = 1$. Now, the likelihood of any capture history can be obtained using these parameters. For example, the likelihood for the capture history 01010 is given by

$$P[(01010)] = [b_0(1-p_1)\varphi_1 + b_1]p_2\varphi_2(1-p_3)\varphi_3 p_4[1-\varphi_4+\varphi_4(1-p_5)].$$

The complete likelihood function is the product of likelihoods of all capture histories. Schwarz and Arnason (1996), showed that it can be partitioned into three separate probabilities

$$\mathcal{L} = P[first\ capture]P[subsequent\ recaptures]P[loss\ on\ capture].$$

These parameters can be obtained using the ML estimation approach. The assumptions (see Table 2) for this model are as follows (Williams *et al.* 2002):

1. The capture probability at a particular capture occasion is the same for all marked and unmarked individuals. Thus, behavioural response to trapping cannot be modelled in this approach and data that have trap response will lead to biased estimates.
2. The survival and entry probabilities are homogeneous across all individuals at any given capture occasion.
3. The survival, capture and entry into the study area of all individuals are independent of each other.

4. All other assumptions of the CJS model given above also apply to POPAN.

1.1.4 Closed population models

Darroch's (1958) work also led to a rich development of closed population models wherein the number of individuals in the study area remains constant during the sampling period. A fundamental synthesis of eight different closed-capture models is presented by Otis *et al.* (1978). These models have only two kinds of parameters, capture probabilities (p) and population size (N), as there are no additions or removals from the population. These models treat capture probabilities either as constant or varying in three different ways, namely, over time (capture occasions), due to behavioural response to trapping, and among individuals. The model with constant capture probabilities, M_0, has only two parameters, N and p. An ML estimator is available for this model (Darroch 1958, Otis *et al.* 1978). The model with time-varying capture probabilities, M_t, has K+1 parameters, N and p_j (for j = 1 to K capture occasions). This model is a K-sample analogue of the Lincoln-Petersen estimator and an ML estimator is available for it (Schnabel 1938, Darroch 1958). The model that accounts for behavioural response to trapping, M_b, has three parameters, N, p_c (probability of capture at first trapping) and p_r (probability of capture at subsequent trappings). Individuals can either be modelled to favour traps more after first capture ($p_c < p_r$; trap happy) or to avoid traps after first capture ($p_c < p_r$; trap shy). Otis *et al.* (1978) provide the ML estimator for this model. The model that accounts for individual heterogeneity in capture probabilities, M_h, has N+1 parameters, N and p_i (for i = 1 to N individuals). ML estimates for this model are not readily available, thus, alternative approaches were put forward. An approach using an underlying probability distribution of the capture probabilities and the generalized jackknife statistic was developed (Burnham and Overton 1978, 1979, Otis *et al.* 1978). Another approach was to use the sample coverage statistic (C). C is the ratio of the sum of capture probabilities of all individuals that are caught to the sum of capture probabilities of all individuals. The estimate of population size is thus

$$\hat{N} = \frac{M_{K+1}}{\hat{C}},$$

where M_{k+1} is the total number of individuals ever caught, and estimators for $\hat{C}$ have been developed (Chao *et al.* 1992, Chao and Lee 1992, Lee and Chao 1994). The above two estimators also apply to models M_{tb} and M_{th}, which allow capture probabilities to vary over time and according to trap response behaviour, or across time and among individuals, respectively. Norris and Pollock (1996) developed a model assuming that there is a mixture of a finite number of groups of capture probabilities. The number of mixtures and the proportion of individuals are unknown and the ML estimate is obtained by using the expectation-maximization (EM) algorithm (Dempster *et al.* 1977) for number of mixtures ranging between M_{k+1} and a predetermined upper-bound on N. The highest ML estimate from the above is then chosen as the non-parametric ML estimate. Pledger (2000) developed a similar approach in which the number of mixtures is given as input, and used that to develop estimators of all eight models (including M_{bh} and M_{tbh}). It was also shown, through simulations and actual data sets, that two-mixture models give parsimonious models and robust estimates (Pledger 2000). This is the approach that is currently used to model heterogeneity in capture probabilities in closed population models (Amstrup *et al.* 2005). Models have also been developed to include data about individual covariates of capture probabilities (Pollock *et al.* 1984, Huggins 1989, 1991, Alho 1990), if such data (e.g. body size, social rank) are also collected. These studies model capture probabilities as a linear-logistic function of the individual covariate.

1.1.5 Robust Design

The survival estimates of the Jolly-Seber open population models do not get biased by individual heterogenity in capture probabilities and permanent trap response, but the estimators for abundance are not robust to these sources of variation in capture probabilities (Gilbert 1973, Carothers 1973, 1979). The Robust Design class of models (Pollock 1982) are a synthesis of the open and closed population models described above that allow modelling of individual and behavioural variation in capture probabilities by using a hierarchical sampling approach. The sampling effort is divided into multiple sets of capture occasions, the sets being called the primary occasions, and the sampling occasions within sets being called the secondary occasions. The capture probabilities and population sizes are estimated over each of the primary occasions by applying the closed population models of Otis *et al.* (1978) to the secondary occasions in each primary occasion. The survival rates are estimated by applying open population models to the primary occasions by grouping each set of secondary occasions into a single primary occasion. New recruits at each primary occasion are estimated using the population size estimates from the closed models, survival rates from the open models, and the following relationship from the open population models

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\varphi}_i \hat{N}_i,$$

where $\hat{B}_i$ is the number of new entrants between occasion *i* and *i*+1. Immigration ($1-\gamma'$) and emigration (γ'') can be separately estimated as well (Kendall *et al.* 1995, 1997). Movement (immigration and emigration) can be modelled to be random ($\gamma' = \gamma''$), null ($\gamma' = 1$; $\gamma'' = 0$) or Markovian (movement depends on the location of the individual in the previous occasion). A full likelihood approach to jointly estimate abundance, survival and capture probabilities has also been developed (Kendall *et al.* 1995, 1997). The work of Norris and Pollock (1996) and Pledger (2000) allows heterogeneity models to also be modelled with full likelihoods. The secondary occasions within each primary occasion can also be modelled using open population models (Schwarz and Stobo 1997, Kendall and Bjorkland 2001).

1.1.6 Multistate models

Multistate models were developed in the context of estimating rates of migration between different areas (states) and, thus, were initially called multisite models (Arnason 1972, 1973). These models were specifically developed for the case with three capture occasions and gave biased estimates for greater than three occasions. In general, a multistate model assumes two or more states (for example, different subpopulations of a metapopulation or different reproductive states) in which an individual can be at any given time, each state being characterized by its own set of capture probabilities and the probabilities of transition from one state to another. Schwarz *et al*. (1993) developed an ML estimator for this model which gave robust estimates for more than three capture occasions. Hestbeck *et al*. (1991) developed a model with Markovian state transition probabilities, i.e., the probability of transition depends upon the state in the previous occasion. An easier implementation of the Arnason-Schwarz model was developed with simple non-Markovian transition probabilities (Brownie *et al*. 1993). The state an individual is in might not be readily ascertainable in the field, say, as in the case of reproductive state. Multievent models were developed to relate states to certain correlated events so that estimates could be found even in the face of incomplete information about the states (Pradel 2005). For example, if state can only be identified reliably for breeders, but not for non-breeders, multievent models can be used to model the finite mixture models that deal with individual heterogeneity (Pledger *et al*. 2003), and estimates of proportion of the population in each mixture can also be obtained (Pradel 2005). Multistate models have been used to study the cost of reproduction on survival rates (Nichols *et al*. 1994) and metapopulation dynamics (Spendelow *et al*. 1995) among other things. Nichols and Kendall (1995) have reviewed how multistate models can be used to answer various questions in evolutionary ecology.

Table 2: Model assumptions and the sources of variation in capture probabilities that the respective models can handle.

Model	Assumptions	Sources of variation in p dealt with
CJS	1. No individual heterogeneity in φ and p 2. Permanent emigration 3. Independence of capture and survival among individuals 4. Instantaneous sampling 5. No tag loss	1. Temporal
JS (POPAN)	1. All assumptions from CJS 2. φ, p and b are the same for all individuals 3. Independence of capture, survival and entry among individuals 4. No tag loss	1. Temporary migration 2. Temporal
Closed capture models (Otis *et al.* 1978)	1. Demographic and geographic closure 2. No tag loss	1. Individual heterogeneity 2. Behavioural response to trapping 3. Temporal 4. Individual covariates
Robust Design	Same as that of closed capture models during primary occasions and Jolly-Seber models across primary occasions	1. Individual heterogeneity 2. Behavioural response to trapping 3. Temporal 4. Temporary migration 5. Individual covariates
Multistate models	1. φ and p are same for all individuals 2. No temporary migration 3. No tag loss 4. Independence of survival and capture among individuals	1. Individual heterogeneity 2. Temporal 3. Behavioural and physiological reasons 4. Location of capture
SECR	1. Demographic and geographic closure 2. Home ranges are randomly distributed 3. Detection is a function of distance from trap 4. Independence of capture among individuals 5. Independence of capture for same individual at different traps	1. Individual heterogeneity due to spatial distribution of individuals and other sources 2. Temporal 3. Behavioural response to trapping 4. Location and other covariates of traps 5. Individual covariates

1.1.7 Spatially-explicit capture recapture models

A different approach to estimating density and abundance for closed populations, that of the spatially-explicit capture-recapture (SECR) models, taking into account the distance of an individual's home range from trapping sites, has also been developed (Efford 2004, Borchers and Efford 2008, Royle *et al*. 2009a,b, Borchers 2012). In SECR models, capture probability is modelled as a function of the distance between location of the individual's home range center to each of the trapping sites. This class of models has two advantages over the standard capture-recapture models. SECR models can account for individual heterogeneity arising from the location of the individual's home range relative to the trap spatial arrangement, and they can also robustly estimate the effective area sampled, thus, giving unbiased density estimates. This additional utility comes at the extra cost of collecting GPS locations of the trapping sites for each capture. SECR models can incorporate variation due to behavioural trap response, individual heterogeneity apart from that induced by home range locations of individuals, and temporal variation in capture probabilities (Royle *et al*. 2014). SECR models for open population data are also being developed (Gardner *et al*. 2010, Royle and Gardner 2010).

1.2 Study Species: the Asian elephant

The Asian elephant (*Elephas maximus*) is a species of megaherbivore and one of the three extant species of Order Proboscidea. Presently ranging from India, through a small part of southern China, to Vietnam, the current range of the Asian elephant is only 6% of its historical range (Sukumar 1989a, Sukumar and Santiapillai 1996, Kemf and Santiapillai 2000), which was a large expanse of over 9 million Km^2 from modern day Iran and Syria to the Yellow River in China (Kemf and Santiapillai 2000, Sukumar 2003). There are an estimated 41,000 to 52,000 Asian elephants present in the world (Sukumar 2003), with India probably harbouring well over 26,000 elephants (Bist 2002, Sukumar 2003). In India, there are four regions of elephant presence: north-western India, north-eastern India, central (eastern) India, and southern India, with population sizes of 1000-1500, 9000-10,000, 1500-2500 and 12,500-14,500, respectively (see AERCC 1998, Bist 2002, Sukumar 2003, Vidya *et al*. 2005). The Asian elephant has been deemed 'endangered' by the IUCN Red List (Choudhury *et al*. 2008) and is also included in Schedule I of the Indian Wildlife (Protection) Act (1972). Despite its conservation status, the Asian elephant has not been well studied outside Sri Lanka and parts of India, and it has been suggested that the global estimates of Asian elephant numbers are nothing more than educated guesses (Kemf and Santiapillai 2000, Blake and Hedges 2004). Thus, it is imperative that more work should be carried out on the demography of Asian elephant populations and, to do that, it is necessary to have a proper framework with which one can robustly estimate demographic parameters such as population size.

1.2.1 Asian elephant ranging and social organization

Asian elephants range over a variety of forest types including dry deciduous, moist deciduous, mixed deciduous, evergreen, and thorn forests (Baskaran 2002, Sukumar 2003). Studies estimating home ranges by direct sighting of female elephant groups found home ranges of over a hundred square kilometres in southern India (105-115 Km^2, Sukumar 1989b, 114-122 Km^2, Kumar *et al*. 2010), but studies estimating female home ranges by radio-collaring elephants have shown much larger home ranges in southern India (562-670 Km^2, Desai and Baskaran 1996) and somewhat larger ranges in a fragmented, relatively small habitat in northern India (184-327 Km^2 in Rajaji National Park, Williams *et al*. 2008). Home range sizes depend on water availability, with home range sizes shrinking during the dry season around perennial water sources, (Sukumar 1989b, Desai and Baskaran 1996, Gaucherel *et al*. 2010, Kumar *et al*. 2010), and on forage availability (Sukumar 1989b, Baskaran *et al*. 2010a, Gaucherel *et al*. 2010). Landscapes that have relatively high diversity of habitat types and availability of water might lead to smaller home ranges as elephants have all the resources that they need in a smaller area (Sukumar 1989b, Gaucherel *et al*. 2010). While some elephants in some populations tend to avoid areas with human disturbance (Fernando *et al*. 2008, Srinivasaiah *et al*. 2012), others might get attracted to human settlements in order to raid crops (Sukumar 1989b, Sukumar 1990, Kumar *et al*. 2010, Srinivasaiah *et al*. 2012).

The basic unit of female social organisation in Asian elephants is the mother-offspring unit (McKay 1973, Kurt 1974), several of which may combine to form 'family groups' (Sukumar 1989a, Fernando and Lande 2000, Vidya and Sukumar 2005). Fernando and Lande (2000) showed that females of a family group shared the same mitochodrial DNA haplotype, validating the female-bonded nature of Asian elephant social organisation. Vidya and Sukumar (2005) showed that 'family groups' comprise related adult females and are probably combinations of mother-daughter, full sisters, and/or half-sisters. Familial social organization has also subsequently been inferred through non-invasive sampling of elephant dung in Laos (Ahlering *et al*. 2011) and in Hassan district, southern India (Chakraborty *et al*. 2014). Associations of multiple family groups, variously referred to as 'bond groups' and 'clans' (as seen amongst African savannah elephants, Douglas-Hamilton 1972, Moss and Poole 1983) were described in Asian elephants also qualitatively (Sukumar 1989a, Baskaran *et al*. 1995). More recently, a study in Sri Lanka showed quantitatively that adult females show non-random long-term associations beyond the family group, thus exhibiting 'fission-fusion' dynamics (de Silva *et al*. 2011a, de Silva and Wittemyer 2012). Fission-fusion societies are those in which there are non-random associations of individuals but no fixed groups, with group sizes changing through splitting of groups (fission) and reassociation of subunits (fusion) (Kummer 1971). While fission-fusion societies were not thought to be common amongst mammals, spatiotemporal grouping patterns form a continuum, and different extents of “fission-fusion dynamics” characterize different mammalian species (see Aureli *et al.* 2008). Based on what is known about African savannah elephants (Douglas-Hamilton 1972, Moss and Poole 1983, Wittemyer *et al.* 2005), elephant family groups have been classified as showing a high degree of fission-fusion dynamics (Aureli *et al.* 2008). The males in Asian elephant society leave their natal groups when they reach adolescence and are thereafter largely solitary (Desai and Johnsingh 1995).

1.2.2 Studies to estimate population sizes in Asian elephants

Initial studies to estimate population abundance or density in Asian elephants largely relied on ‘total’ direct counts of elephants or direct counts of elephants in forest blocks, and on direct or indirect (through dung and other signs of elephant) counts of elephants from line transects (for example, Dawson 1990, Karanth and Sunquist 1992, Varman *et al.* 1995, see Burnham *et al.* 1980 for line transect methodology). Several subsequent estimates of density, especially by the forest and wildlife departments, have continued to be based on block counts (for example, Baskaran and Sukumar 2011) or direct or indirect counts from line transects (for example, Baskaran *et al.* 2010b). Abundance of elephant males in the Rajaji National Park in northern India was estimated using mark-resight methods (Bowden and Kufeld 1995) and total abundance calculated using the proportion of males in the total population (Williams *et al.* 2007). Mark-resight methods have also been used subsequently to estimate the abundance of adult males in Nagarahole and Bandipur National Parks in southern India, using the POPAN open population mark-recapture model, and total population size calculated using the proportion of adult males in the entire population (Goswami *et al.* 2007). Adult female abundance and density and elephants in the Uda Walave NP, Sri Lanka, was estimated using mark-resight and the Robust Design and SECR models (de Silva *et al*. 2011b). During the last decade, dung-extracted DNA has also been used to estimate Asian elephant population sizes, either as minimum population sizes (Vidya *et al*. 2007, Chakraborty *et al*. 2014) or in the form of estimates from a capture-mark-recapture framework (Hedges *et al*. 2013, Gray *et al*. 2014).

Direct block counts are not very reliable as they do not yield reliable estimates when detection probabilities are less than 1. Direct and indirect counts from line transects do not yield reliable estimates if the population is open or if distance measurements are imprecise (Williams *et al*. 2002). Studies in India that have used mark-recapture methods have only estimated male abundance using these methods, and estimate total abundance by using proportion of males in total sightings (Goswami *et al*. 2007, Williams *et al*. 2007), an approach that is not very reliable. Only three studies (de Silva *et al*. 2011b, Hedges *et al*. 2013, Gray *et al*. 2014) have estimated total population sizes using mark-recapture techniques, but these studies assumed independent detection probabilities among individuals. This assumption is usually violated when sampling female groups in elephants visually and also through fecal sampling as individuals in a group will often defecate at the same time at some locations (Nandini Shetty *et al*., personal communication). Females might also have an additional source of individual variation in capture probabilities through their dominance hierarchy and ranks (Cubaynes *et al*. 2010). Such populations can still be sampled by considering the unit of sampling to be fixed female groups rather than individuals, and later multiplying the estimate of number of groups with average group size (Williams *et al*. 2002). However, this is not possible in species such as the Asian elephant that show fission-fusion dynamics, in which group identities are not conserved over time.

The objective of this study was, therefore, to implement an individual-based simulation model with different social structures that could be used to see how robust mark-recapture population size estimators are when they are used on data from species that live in groups and show fission-fusion dynamics, such as elephants. The robustness of these estimators were also checked for populations with fixed groups and populations with non-associating individuals. I have used the term non-associating instead of solitary because solitary individuals in the wild might actively avoid one another and space themselves out, but no such avoidance was modelled into the simulation. The mark-recapture models assume independence between captures of individuals, but, in the fission-fusion and the fixed group social structures this assumption is not met. Thus, it was expected that the most robust estimates should be obtained in the case of non-associating individuals followed by fixed groups and groups showing fission-fusion dynamics. The effects of varying trap densities, trap spatial arrangement (uniform and random), density of individuals and spatial scale of sampling were also studied for the mark-recapture estimators. It was expected that more robust estimates should be obtained for higher trap densities and higher density of individuals as capture probabilities would be higher in these cases (Otis *et al.* 1978). Uniform trap spatial arrangements were expected to give less variable estimates over multiple samplings. Individuals living near the edges of the trap spatial arrangement would have lower capture probabilities that the ones living in the interior: thus, larger scale of sampling area was expected to reduce individual hetergeneity in capture probabilities due to the reduction in edge length to total area ratio. The models that were compared for all these effects were POPAN and Robust Design with heterogeneity in capture probabilities. It was expected that the Robust Design model with heterogeneity would perform better than POPAN. Other methods of population estimation were not tested for want of time and will be tested in the future.

CHAPTER 2: METHODS

2.1 Simulation

2.1.1 Overview

As described in the Introduction, the objectives of this study were to assess two standard mark-recapture estimators of population size, POPAN and Robust Design with heterogeneity, in the face of differences in the social structure of a species, population densities, trap densities, trap spatial arrangement, and sampling scale. These factors are expected to alter the probability of detection of individuals in the manner described in the Introduction. I focused specifically on Asian elephants because they are one of the few species in which females live in a multi-level group structure that shows fission-fusion dynamics (de Silva *et al*. 2011a, de Silva and Wittemyer 2012) and for which robust population size estimates are often not available (Kemf and Santiapillai 2000, Blake and Hedges 2004). Multi-level group structure and fission-fusion dynamics results in variation among individuals in the probability of detection and non-independence of probabilities of detection of different individuals. In this chapter, I describe an individual-based simulation model that I developed to provide a framework within which the mark-recapture estimators of population size could be evaluated for an elephant population in which the movement of individual elephants could be simulated based on three different social structures, giving rise to different patterns of among-individual variation in capture probability. The three kinds of social structure modelled in this framework are a fission-fusion type of society, a society with fixed groups, and a population of non-associating individuals (see Introduction for details).

The simulation model focused on adult females because Asian elephants live in female-bonded groups (Fernando and Lande 2000, Vidya and Sukumar 2005, Ahlering *et al*. 2011), and show movement that is non-independent of that of other females. Adult males lead largely solitary lives (Desai and Johnsingh 1995). The ranges(s) of parameter values in the simulations were roughly based on the Asian elephant population inhabiting the Nilgiris-Eastern Ghats Reserve, southern India, in general and, for some values, Nagarahole and Bandipur National Parks within the Nilgiris-Eastern Ghats Reserve, specifically. The Nilgiris-Eastern Ghats Reserve holds the world's single largest population of Asian elephants, numbering over 9000 individuals (AERCC 1998). The density of elephants in the Nilgiris-Eastern Ghats Reserve is thought to range from 0.5 to 0.83 elephants Km^{-2} (AERCC 1998) and that in Nagarahole National Park ($11^o50'$-$12^o15'$ N; $76^o0'$-$76^o15'$ E) has been estimated at 2.25 (AERCC 1998) to 3.3 elephants Km^{-2} (Karanth and Sunquist 1992). Individual-based identification and ageing of elephants in Nagarahole and Bandipur National Parks showed that about 47% of the elephant population are adults (>=15 years of age), of which about 35% were adult females (Nandini Shetty, Keerthipriya P, Vidya TNC, unpublished data), yielding an adult female density of about 0.18-0.3 (based on the Nilgiris-Eastern Ghats Reserve elephant density) to 0.79-1.16 (based on Nagarahole National Park elephant density) adult female elephants Km^{-2}. Therefore, adult female densities of 0.2, 0.4, and 0.8 adult female elephants Km^{-2} were used in different runs of the simulation. An average home range size of about 600 Km^2 was considered based on a study of radio-collared female elephants in the Nilgiris-Eastern Ghats Reserve (Baskaran *et al.* 1995). The total study area was taken to be 2500 Km^2 as a balance between including a sufficient number of home ranges and the time taken to run the simulation. The size of Nagarahole and Bandipur National Parks together is about 1500 Km^2.

For each of the adult female densities, the movement of individuals over a period of one year was simulated in a manner that reflected how the specific social structure used would affect coordinated movement among adult females. The process of trapping for mark-recapture was also simulated, using six combinations of two spatial arrangements and three densities of traps. Ten replicate simulations were run for various combinations of trap spatial arrangement, trap density, overall adult female density, and social structure. The possible effects of spatial scale of sampling were also examined by running simulations with three different sizes of sampling blocks (see section 2.1.5) within which sampling was done. Capture histories (see Introduction) were then generated from these simulations and were used to get mark-recapture estimates of population size. The efficacy of these estimates was assessed by calculating the relative bias (section 2.2.2) in these estimates, using the real population sizes from the simulation. Subsequent analyses examined the effects and interactions of social structure, trap spatial arrangement, trap density, overall adult female density, and the spatial scale of sampling on the relative bias of the mark-recapture estimators. The simulation was programmed and run using MATLAB® R2011a (The MathWorks® Inc. 2011).

2.1.2 Initialization

The parameters that were variable across simulation runs were trap density, spatial scale of sampling, the structure of AI values to simulate different social structures, and overall adult female density. For each combination of the above variables, the trap spatial arrangement was either spatially uniform or spatially random (following a uniform random distribution). The different values of each of these parameters used in the simulations are listed in Table 2.1. The total study area was 2500 Km^2 (50 Km × 50 Km). The total number of groups was set to one-fifth of the total female count (i.e., adult female density), and the total number of clans to one-thirtieth of the total female count. Each group was randomly assigned a group size, which was rounded off to the nearest integer, from a normal distribution with a mean of five and a standard deviation of 2.33. This gave a slightly different total individual count than the original (i.e. based on 1/5th of female density) and this new count was then used subsequently in the simulation. A group identity was assigned to all the members of each group. Each clan was assigned a clan size (number of groups) from a uniform integer distribution ranging from four to eight. The total number of groups was constrained to remain equal to the original value because the total number of groups assigned using the above method would not always be the same as the original number of groups. A clan identity was assigned to all individuals in a number of groups equal to the respective clan size. Each pair of individuals was assigned an AI value as described in section 2.1.3. Each clan was assigned a rectangular home range of an area of 600 Km^2, with a randomly assigned home range center, and a randomly generated length:breadth ratio between 0.5 and 2. Each group was assigned an initial random group location within its clan home range, and all individual members of a group were randomly assigned initial positions within a 500 m radius of the initial group location, as animals within a group are likely to range within this distance (de Silva *et al.* 2011a, Shetty *et al.*, unpublished data from Nagarahole-Bandipur). Trap locations were initialized considering the type of trap spatial arrangement in that particular simulation. Traps were either placed in a uniform grid of dimensions √(Total Traps) × √(Total Traps) within each area sampled (sampling block, see 2.1.5 below), or they were given random locations within each sampling block based on a uniform random distribution.

2.1.3 Social Structures

Three different social structures were used in the simulations – groups within clans, only clans, and solitary individuals. These were differentiated amongst themselves only by changing the pattern of initially assigned pair-wise association index (AI) values. AI is an index that estimates the extent of association between two individuals and can be calculated in different ways. We used the Simple Ratio method (see Ginsberg and Young 1992), which results in AI values between zero and one, zero indicating no association between a pair of individuals and one indicating complete association. Pairs of individuals with different social relationships were assigned AI values from uniform distributions of different ranges. These different combinations of ranges for each social structure are given in Table 2.1. The AI values for the groups-within-clans type of social structure ensured that, while moving, the probability of an individual moving towards a member of its group was the highest, the probability of moving towards a member of its clan but not group was the second highest, and the probability of moving toward an unrelated individual (not from its clan) was the lowest. The AI values for only-clans type of social structure ensured that individuals had the same high probability of moving toward a member of either their group or other groups within the clan (thus, in effect, eliminating group structure), and a low probability of moving toward individuals not from its clan. The AI values for the non-associating-individuals type of social structure ensured that individuals had a low probability of moving toward any other individual irrespective of the initially assigned relationship through group and clan identity (thus, in effect, eliminating group and clan structures).

2.1.4 Movement Algorithm

Positions of individuals were updated in time increments of two hours, over 365 days in the following manner. The update, which was implemented iteratively by taking each individual, one at a time, to be the focal individual, consisted of first finding individuals that were within the auditory range (2 Km, see Payne *et al.* 1986) of the focal individual. For each of these individuals in the auditory range, the focal individual was assigned a probability that it would move towards the other individual, and this probability was proportional to the pair-wise AI between the focal individual and the other individual. The exact probabilities were calculated by normalizing the pair-wise AI between each individual in the auditory range and the focal individual by the sum of AIs between all individuals in the auditory range and the focal individual. One target individual was then chosen according to this multinomial probability distribution. The focal individual was then either moved towards the chosen target individual with a probability equal to their pair-wise AI, or moved in a uniformly random direction with a probability of (1 – AI), at a constant speed of 5 Km/day (5/24 Km/Hour). If there were no individuals in the auditory range of the focal individual, the focal individual was moved in a uniformly random direction with the same constant speed. If the focal animal's updated position was outside its clan home range, then it was moved in a direction towards the center of the home range with the same constant speed as above. A two-hour time step was deemed complete when the positions of all individuals had been updated.

Fission-fusion dynamics in the simulations were confirmed by finding out whether individuals were assigned to different spatial clusters across days. Clusters were obtained using the K-means clustering algorithm (MacQueen 1967, Seber 1984) on individuals' spatial coordinates. Clustering was done for $k = 2$ to the total number of groups, and a mean silhouette (Rousseeuw 1987) value was calculated for each case. The k with the highest mean silhouette was chosen, clusters within this case that had silhouettes less than 0.9 were identified, and then clustering was redone for $k = 2$ to (the total selected clusters x 1.5). One-and-a-half times the selected number of clusters was used to give a high enough ceiling to k so that the best possible k could be within this range. The k with the highest mean silhouette was again chosen and this clustering was merged with the original clustering. Then, any individuals found in the same cluster were said to be associating.

2.1.5 Trapping Individuals

The total study area in the simulation was gridded into blocks of three different sizes such that the study area was divided equally into 16, 9, or 4 blocks, respectively. This was done so that a partial sampling of the total area (as one would expect in a field study) could be simulated at different spatial scales. Two kinds of spatial trap spatial arrangement, uniform and random, were used for all the various combinations of different spatial scales of sampling (block size), trap density, adult density and social structure. A step function was used as the detection function, i.e., all individuals within a 100 m radius of a particular trap were recorded as sighted at that trap, and any individuals outside this radius were not. Sampling was done for 1 week every 30 days starting from day 15. The simulation was allowed to run for 14 days so that the movement patterns had time to stabilize after the random initialization of group positions. Capture histories were then created for various analyses within each block. Moreover, the density of females over the entire simulation period, over the entire sampling period, and over each week of sampling, for each block was calculated. The area of each block was taken to be 2500/[total number of blocks in that case] Km^2. The total number of unique individuals (i.e., no repeat sightings were recorded) seen in a block was recorded over the entire simulation period, over each week of sampling, and over the entire sampling period. These were later used as the real population sizes in various analyses of relative bias in population size estimation as described in section 2.2. The actual densities from the above calculations were used as a factor in analysis of variance (ANOVA) of relative bias (see Section 2.2.2), the factor levels being density less than 0.3 and density greater than or equal to 0.3.

Table 2.1. Different cases of parameter values used for trap density, sampling scale, social structure and overall adult female density used in the simulations in all combinations. For social structure, Case 1 is groups-within-clans, Case 2 is only-clans and Case 3 is non-associating (solitary) individuals.

Parameter		Case 1	Case 2	Case 3
Trap Density		0.05 traps/Km^2	0.5 trap/Km^2	1 traps/Km^2
Sampling Scale		16 blocks	9 blocks	4 blocks
Social Structure (AI range)	Group mates	0.5-0.7	0.5-0.7	0-0.1
	Clan mates	0-0.2	0.5-0.7	0-0.1
	Other individuals	0-0.001	0-0.001	0-0.001
Individual (adult female) Density		0.2 individual/Km^2	0.4 individuals/Km^2	0.8 individuals/Km^2

2.2 Analyses

2.2.1 Population size estimation

The estimation of population sizes using the POPAN and Robust Design models was done in RMark (Laake 2013) which is a programmable interface to Program MARK (White and Burnham 1999), written in the R programming language (R Core Team 2014).

2.2.1.1 POPAN

The POPAN model has three types of parameters, namely, survival probability (φ), capture probability (p) and probability of immigration into the study area from the superpopulation (*pent* or b). The superpopulation is defined as the total number of animals that ever enter the study area during the sampling period. The three kinds of parameters can be modelled to vary over time or can be kept constant. I used a constant probability of survival over sampling occasions, as deaths were not modelled in the simulation. The probability of survival was, however, not fixed at 1, because emigration from the study area was accounted for as a decrease in the survival probability. Not considering deaths is reasonable since only adult females were considered in the simulation, and the mortality rate of adult elephants in a single year is quite low if poaching of males for ivory is excluded (see Sukumar 1989a, Sukumar *et al*. 1998). I used a constant probability of capture and of entry, as the overall movement of groups was essentially uniformly random in the simulation. The population size was estimated over all 84 occasions (12 seven day intervals) in the capture history. As there was a gap of 23 days in the sampling after every 7 days, this time interval was explicitly defined in the model so that the survival probabilities between each 7 day period were adjusted to be over 23 days as opposed to only one day. The estimation for the above specified model was done using RMark for capture histories obtained from each block within each replicate simulation.

2.2.1.2 Robust Design with individual heterogeneity

As described in the Introduction, Robust Design employs a hierarchical sampling approach with multiple sets of sampling occasions, with each set demographically and geographically closed, i.e., no additions or removal of individuals is allowed within the duration of each set. The sets are called primary occasions and the sampling occasions within them are called secondary occasions. Thus, each set of secondary occasions is closed to additions and removals from the study population, but the intervals between the primary occasions are open to additions and removals from the study population. The Robust Design model with heterogeneity assumes the population to be a finite mixture of two or more types of individuals with different capture probability (Norris and Pollock 1996, Pledger 2000). Robust Design models are built upon several parameters, namely survival probabilities (φ), capture probability, probability of immigration ($1-\gamma'$) (γ' is the probability that an individual was outside the study area in the previous occasion and remains outside in the current occasion as well), probability of emigration (γ'') (γ'' is the probability that an individual was within the study area in the previous occasion and moves outside during the interval between the previous and the current occasions) and population sizes for each primary occasion (N). I used a constant probability of survival (φ) over sampling occasions as I assumed no death in the simulation. For the two mixture case of the Robust Design with heterogeneity, the proportion of individuals with the first capture probability is given by π for any given occasion, and the proportion of individuals with the other capture probability is ($1-\pi$). I used two mixtures (see Introduction and Pledger 2000) with proportion of individuals in the first mixture (π) set to be constant. Capture probabilities were modelled to be constant over time but to be different for the two mixtures. I used constant Markovian movement to model the two movement parameters, i.e., γ' and γ'' were both set to be constant over sampling occasions. There were 12 primary occasions in all (months), each comprising of seven secondary occasions (days). The analysis of this model through RMark gave a population size for each primary occasion.

2.2.2 Relative Bias

Relative bias in the estimate of population size was calculated as

$$\frac{\hat{N} - N_r}{N_r},$$

where N_r is the real population size of the targeted population and $\hat{N}$ is the estimated population size. Relative bias was calculated for each estimate of population size in each of the simulations for all blocks and replicates. The mean of relative bias was taken across the blocks for each replicate simulation and these replicate means were then used in 4-factor fully factorial analyses of variance (ANOVA) with trap spatial arrangement, trap density, social structure and adult female density as fixed factors crossed with one another. This analysis was done separately for each spatial scale of sampling. The same analysis was also done taking actual densities from the simulation (see section 2.1.5) as a factor instead of initial adult female densities. All ANOVAs were implemented in Statistica version 5.0 (StatSoft 1996). The actual superpopulation size for the POPAN analysis was taken as the total number of unique individuals present in a block throughout the sampling period (no. of days = 84). The actual population size for the Robust Design analysis was taken as the number of unique individuals present within each block during each of the primary occasions (12 primary occasions with seven secondary occasions each).

CHAPTER 3: RESULTS AND DISCUSSION: POPAN ANALYSIS

3.1 Results

Analyses of variance (ANOVAs) on relative bias, averaged across blocks, for each replicate run of the simulations were performed separately for data from each spatial scale of sampling (i.e., 16 blocks, nine blocks and four blocks), and also considering either actual adult female density (<0.3 and ≥0.3 individuals Km^{-2}) or initial adult female density (0.2, 0.4 and 0.8 individuals Km^{-2}) as the factor adult female density. Thus, six four-factor completely randomized ANOVAs were done for the data from POPAN analysis of the simulated data sets: three spatial scales of sampling × two ways of treating adult female density. The four factors considered in each ANOVA were spatial trap arrangement (uniform and random), trap density (0.05, 0.5 and 1.0 traps Km^{-2}), social structure (fission-fusion, fixed clans, and non-associating individuals), and adult female density (with either two or three levels, as described above). The results of the ANOVAs are summarized in Tables 3.1 – 3.6.

Overall, superpopulation sizes were almost always underestimated by the POPAN estimator. However, the pattern of effects of the different factors on relative bias of the POPAN estimator was broadly similar, regardless of whether the analyses used initial adult female density or the actual adult female density in the blocks in the simulations (compare Figures 3.1 and 3.4, 3.2 and 3.5, and 3.3. and 3.6, respectively). A majority of the variation in relative bias was ascribable to variation in trap spatial arrangement and trap density, with these two main effects accounting for about 60-80% of the total sums of squares (TSS) in all six ANOVAs (Table 3.7). The contribution of error sums of squares (ESS) to TSS varied systematically, increasing from 4.1% to 8.2% to 11.1% of TSS, as the number of blocks reduced from 16 to 9 to 4, when using actual adult female density, and from 6.8% to 14.4% to

17.4% of TSS, as the number of blocks reduced from 16 to 9 to 4, when using initial adult female density. This is likely due to the fact that superpopulation sizes per block will be larger as the number of blocks decreases since the total area used in the simulations is constant. Therefore, once averaged among blocks within each replicate, the variation across replicates will be among larger superpopulation sizes in the case of four blocks, followed by the nine and 16 blocks cases, respectively, yielding the observed pattern of ESS contributing increasingly to TSS as the number of blocks decreases.

Among the main effects, trap spatial arrangement and trap density, as well as the interaction between them, were significant in all the six ANOVAs (Tables 3.1-3.6). On an average, the random trap arrangement yielded substantially better estimates of superpopulation size, often by a factor of two or three (Figures 3.1-3.6, Table 3.8), than the uniform trap arrangement, with highly significant ($P<0.001$) main effects in all six ANOVAs (Tables 3.1-3.6). However, trap arrangement also showed highly significant ($P<0.001$) interactions with trap density across all six ANOVAs (Tables 3.1-3.6), with no difference in the patterns of trap spatial arrangement x trap density interactions between analyses using actual adult female density and the initial adult female density (Table 3.9). The differences in relative bias between uniform and random trap arrangements tended to be much smaller at the lowest trap density of 0.05 Km^{-2} than the higher trap densities of 0.5 Km^{-2} or 1 Km^{-2}, with the mean relative bias not differing significantly between uniform and random trap arrangements at the lowest trap density of 0.05 Km^{-2}, except in the cases of four blocks with initial or actual adult female density (Figures 3.1-3.6, Table 3.9). The lowest trap density (0.05 traps Km^{-2}) typically yielded the poorest estimates of superpopulation size, compared to either 0.5 or 1.0 traps Km^{-2} (Figures 3.1-3.6, Tables 3.1-3.6, Table 3.8). The pattern of pairwise significance in relative bias across pairwise trap densities remained the same irrespective of whether actual adult female density or initial adult female density was used (Table 3.8). When trap density was increased from 0.05 traps Km^{-2} to 0.5 traps Km^{-2}, there was a greater decrease in the absolute values of bias in the cases with random trap arrangement than in the cases with uniform trap arrangement (Figures 3.1-3.6, Table 3.9). When trap density was increased from 0.5 traps Km^{-2} to 1 trap Km^{-2}, there was no further improvement in absolute values of bias while using either uniformly placed or randomly placed traps in different spatial scales, with the exception of random traps at a spatial scale of 16 blocks (Figures 3.1, 3.4, Table 3.9).

Adult female density also showed highly significant ($P<0.001$) main effects in all six ANOVAs (Tables 3.1-3.6), regardless of whether initial or actual adult female densities were used. In both cases, the low density yielded the larger values of relative bias (Figures 3.1-3.6). In the case of actual densities, the ≥0.3 individuals Km^{-2} density yielded relative bias values about 40% smaller than the <0.3 individuals Km^{-2} case across all three spatial scales (Figures 3.1-3.3, Table 3.8). In the case of initial densities, the 0.4 and 0.8 individuals Km^{-2} densities yielded about 10-20% lower relative bias, respectively, than the 0.2 individuals Km^{-2} density (Figures 3.4-3.6, Table 3.8). The trap density x adult female density interaction was also highly significant ($P<0.001$) in all six ANOVAs (Tables 3.1-3.6), regardless of whether initial or actual adult female densities were used. In the case of actual adult female density, the pattern of significant pairwise differences did not vary much across spatial scales (Table 3.10). The largest reduction in bias at high adult female density was typically seen at the lowest trap density of 0.05 Km^{-2}, with smaller and not very different reductions in bias at high adult female density being seen at trap densities of 0.5 and 1 Km^{-2} (Figures 3.1-3.3, Table 3.10). In the case of initial adult female densities, too, the pattern of significant pairwise differences did not vary much across spatial scales (Table 3.10). The general trend was for relative bias to significantly increase with each stepwise increase in adult density at the lowest trap density of 0.05 Km^{-2}. At the two higher trap densities of 0.5 and 1 Km^{-2}, however, the mean relative bias did not, on the whole, vary significantly across the different adult densities x trap density combinations (Figures 3.4-3.6, Table 3.10).

Social structure showed significant (*P*<0.05) main effects in four of the six ANOVAs, with significant effects in the 16 and 4 blocks cases but no significant effect in the nine blocks cases (Tables 3.1-3.6). The lack of significance of social structure as a main effect in the nine blocks cases was not due to any dramatic increase in the sums of squares due to interactions involving social structure in these cases. While the above main effects of social structure remained unchanged regardless of whether initial or actual adult female densities were used, higher significance was seen in the 16 blocks case when actual adult female densities were used (*P*<0.01) than when initial female densities were used, while this was reversed in the 4 blocks case, with higher significance observed when initial female densities were used (Tables 3.1, 3.3-3.4, 3.6). Non-associating individuals consistently showed the lowest relative bias in the cases where social structure had a main effect (Table 3.8). Non-associating individuals showed significantly lower bias than groups within clans but did not differ in their bias from only clans in the 16 blocks cases, while the opposite was true in the four blocks cases, with non-associating individuals showing significantly lower bias than only clans and no difference in their bias from groups within clans (Table 3.8). In all these four cases, there was no significant difference (*P*>0.05) in relative bias between groups within clans and only clans (Table 3.8).

There was a significant effect of social structure x trap spatial arrangement in the nine and four blocks cases but not in the 16 blocks case, regardless of whether the actual or initial adult female densities were used (Tables 3.1-3.6). In these (9 and 4 block) cases, there was no effect of social structure on relative bias when traps were randomly placed, while there was a significant effect of social structure on relative bias when traps were uniformly placed (Figures 3.2-3.3, 3.5-3.6, Table 3.9). With the latter trap arrangement, non-associating individuals showed less bias than groups within clans and only clans in the four blocks case, non-associating individuals showed less bias than only clans in the nine blocks case with actual adult female density, and there was no difference across social structures in the nine blocks case with initial adult female density (Table 3.9). There were also significant interactions between social structure and trap density in the 16 blocks and nine blocks cases, but not in the four blocks cases, irrespective of actual or initial adult female densities being used, and between social structure and actual adult female density but not initial adult female density in the 16 blocks and four blocks cases (Tables 3.1-3.6). In the 16 blocks cases with actual and initial adult female densities, non-associating individuals showed the highest bias at the lowest trap density (0.05 traps Km^{-2}), but tended to show the lowest bias at higher trap densities of 0.5 or 1.0 traps Km^{-2} (Figures 3.1, 3.4, Table 3.11). This pattern was less pronounced in the nine blocks cases (Figures 3.2, 3.5, Table 3.11). However, there were two three-way interactions involving social structure (trap density x social structure x adult female density, and trap spatial arrangement x social structure x adult female density) in the nine blocks case with actual adult female density (Table 3.2). This can be seen as a greater difference between the bias for non-associating individuals and the other social structures while using the uniform trap spatial arrangement compared to the random trap spatial arrangement at higher trap densities and actual adult female density (Figure 3.2). In the two cases (16 and four blocks) where there were significant interactions between social structure and actual adult female density, there was a lower bias at the higher adult density (Figures 3.1, 3.3, Table 3.11).

Although social structure had significant main effects and some significant interactions with other factors as described above, the main effects of social structure, along with interactions involving social structure, accounted for only about 2-3.5% of TSS in the ANOVAs (Table 3.7). Thus, social structure was not a large contributer to the relative bias values from the POPAN analyses, with the mean relative biases not being very different from one another based on social structure (Table 3.8).

Table 3.1. ANOVA table for sampling scale of 16 blocks with actual female density as a factor. The dependent variable is relative bias. Factors that showed significant effects are shown in bold font.

Factor	Effect		Error		F	P value
	df	MS	df	MS		
Trap Spatial Arrangement (TSA)	1	6.173	324	0.005	1141.440	<0.001
Trap Density (TD)	2	12.748	324	0.005	2357.444	<0.001
Social Structure (SocS)	2	0.0317	324	0.005	5.859	0.003
Actual Female Density (AFD)	1	5.251	324	0.005	971.014	<0.001
TSA x TD	2	1.235	324	0.005	228.396	<0.001
TSA x SocS	2	0.016	324	0.005	2.946	0.054
TD x SocS	4	0.106	324	0.005	19.515	<0.001
TSA x AFD	1	0.151	324	0.005	27.870	<0.001
TD x AFD	2	0.157	324	0.005	28.945	<0.001
SocS x AFD	2	0.048	324	0.005	8.958	<0.001
TSA x TD x SocS	4	0.008	324	0.005	1.407	0.231
TSA x TD x AFD	2	0.071	324	0.005	13.138	<0.001
TSA x SocS x AFD	2	0.012	324	0.005	2.303	0.102
TD x SocS x AFD	4	0.071	324	0.005	13.102	<0.001
TSA x TD x SocS x AFD	4	0.011	324	0.005	2.113	0.079

Table 3.2. ANOVA table for sampling scale of nine blocks with actual female density as a factor. The dependent variable is relative bias. Factors that showed significant effects are shown in bold font.

Factor	Effect		Error		F	P value
	df	MS	df	MS		
Trap Spatial Arrangement (TSA)	1	8.895	324	0.010	924.708	<0.001
Trap Density (TD)	2	7.455	324	0.010	775.049	<0.001
Social Structure (SocS)	2	0.010	324	0.010	1.048	0.352
Actual Female Density (AFD)	1	5.446	324	0.010	566.199	<0.001
TSA x TD	2	1.627	324	0.010	169.108	<0.001
TSA x SocS	2	0.069	324	0.010	7.134	<0.001
TD x SocS	4	0.087	324	0.010	9.016	<0.001
TSA x AFD	1	0.345	324	0.010	35.909	<0.001
TD x AFD	2	0.433	324	0.010	45.024	<0.001
SocS x AFD	2	0.022	324	0.010	2.259	0.106
TSA x TD x SocS	4	0.013	324	0.010	1.400	0.234
TSA x TD x AFD	2	0.164	324	0.010	17.043	<0.001
TSA x SocS x AFD	2	0.043	324	0.010	4.503	0.012
TD x SocS x AFD	4	0.026	324	0.010	2.691	0.031
TSA x TD x SocS x AFD	4	0.019	324	0.010	2.000	0.094

Table 3.3. ANOVA table for sampling scale of four blocks with actual female density as a factor. The dependent variable is relative bias. Factors that showed significant effects are shown in bold font.

Factor	Effect		Error		F	P value
	df	MS	df	MS		
Trap Spatial Arrangement (TSA)	1	16.964	324	0.013	1335.979	<0.001
Trap Density (TD)	2	3.832	324	0.013	301.806	<0.001
Social Structure (SocS)	2	0.050	324	0.013	3.901	0.021
Actual Female Density (AFD)	1	3.267	324	0.013	257.292	<0.001
TSA x TD	2	0.587	324	0.013	46.206	<0.001
TSA x SocS	2	0.050	324	0.013	3.929	0.021
TD x SocS	4	0.013	324	0.013	1.053	0.380
TSA x AFD	1	0.015	324	0.013	1.205	0.273
TD x AFD	2	0.971	324	0.013	76.476	<0.001
SocS x AFD	2	0.159	324	0.013	12.506	<0.001
TSA x TD x SocS	4	0.152	324	0.013	12.005	<0.001
TSA x TD x AFD	2	0.198	324	0.013	15.587	<0.001
TSA x SocS x AFD	2	0.013	324	0.013	1.010	0.365
TD x SocS x AFD	4	0.004	324	0.013	0.293	0.883
TSA x TD x SocS x AFD	4	0.060	324	0.013	4.762	<0.001

Table 3.4. ANOVA table for sampling scale of 16 blocks with initial female density as a factor. The dependent variable is relative bias. Factors that showed significant effects are shown in bold font.

Factor	Effect		Error		F	P value
	df	MS	df	MS		
Trap Spatial Arrangement (TSA)	1	8.498	486	0.008	1090.485	<0.001
Trap Density (TD)	2	18.553	486	0.008	2380.722	<0.001
Social Structure (SocS)	2	0.029	486	0.008	3.741	0.024
Initial Female Density (IFD)	2	0.571	486	0.008	73.231	<0.001
TSA x TD	2	1.872	486	0.008	240.212	<0.001
TSA x SocS	2	0.017	486	0.008	2.149	0.118
TD x SocS	4	0.160	486	0.008	20.521	<0.001
TSA x IFD	2	0.011	486	0.008	1.368	0.256
TD x IFD	4	0.045	486	0.008	5.768	<0.001
SocS x IFD	4	0.005	486	0.008	0.696	0.595
TSA x TD x SocS	4	0.014	486	0.008	1.754	0.137
TSA x TD x IFD	4	0.002	486	0.008	0.259	0.904
TSA x SocS x IFD	4	0.013	486	0.008	1.671	0.156
TD x SocS x IFD	8	0.007	486	0.008	0.908	0.509
TSA x TD x SocS x IFD	8	0.009	486	0.008	1.122	0.347

Table 3.5. ANOVA table for sampling scale of nine blocks with initial female density as a factor. The dependent variable is relative bias. Factors that showed significant effects are shown in bold font.

Factor	Effect		Error		F	P value
	df	MS	df	MS		
Trap Spatial Arrangement (TSA)	1	12.929	486	0.015	883.422	<0.001
Trap Density (TD)	2	11.084	486	0.015	757.377	<0.001
Social Structure (SocS)	2	0.009	486	0.015	0.621	0.538
Initial Female Density (IFD)	2	0.402	486	0.015	27.436	<0.001
TSA x TD	2	2.332	486	0.015	159.342	<0.001
TSA x SocS	2	0.101	486	0.015	6.906	0.001
TD x SocS	4	0.125	486	0.015	8.556	<0.000
TSA x IFD	2	0.016	486	0.015	1.101	0.333
TD x IFD	4	0.135	486	0.015	9.227	<0.001
SocS x IFD	4	0.005	486	0.015	0.326	0.861
TSA x TD x SocS	4	0.022	486	0.015	1.473	0.209
TSA x TD x IFD	4	0.002	486	0.015	0.170	0.954
TSA x SocS x IFD	4	0.024	486	0.015	1.650	0.160
TD x SocS x IFD	8	0.005	486	0.015	0.308	0.963
TSA x TD x SocS x IFD	8	0.010	486	0.015	0.688	0.702

Table 3.6. ANOVA table for sampling scale of four blocks with initial female density as a factor. The dependent variable is relative bias. Factors that showed significant effects are shown in bold font.

Factor	Effect		Error		F	P value
	df	MS	df	MS		
Trap Spatial Arrangement (TSA)	1	25.029	486	0.018	1395.961	<0.001
Trap Density (TD)	2	5.441	486	0.018	303.464	<0.001
Social Structure (SocS)	2	0.086	486	0.018	4.824	0.008
Initial Female Density (IFD)	2	0.546	486	0.018	30.457	<0.001
TSA x TD	2	0.821	486	0.018	45.783	<0.001
TSA x SocS	2	0.087	486	0.018	4.875	0.008
TD x SocS	4	0.021	486	0.018	1.172	0.322
TSA x IFD	2	0.079	486	0.018	4.430	0.012
TD x IFD	4	0.160	486	0.018	8.951	<0.001
SocS x IFD	4	0.041	486	0.018	2.282	0.060
TSA x TD x SocS	4	0.232	486	0.018	12.913	<0.001
TSA x TD x IFD	4	0.028	486	0.018	1.583	0.177
TSA x SocS x IFD	4	0.036	486	0.018	2.028	0.089
TD x SocS x IFD	8	0.016	486	0.018	0.905	0.512
TSA x TD x SocS x IFD	8	0.018	486	0.018	0.980	0.451

Table 3.7. Fraction of Sums of Squares from the six four-way ANOVAs.

Effect	**16 Blocks, Actual Density**	**16 Blocks, Initial Density**	**9 Blocks, Actual Density**	**9 Blocks, Initial Density**	**4 Blocks, Actual Density**	**4 Blocks, Initial Density**
TSA	0.144	0.153	0.234	0.262	0.459	0.498
TD	0.596	0.669	0.392	0.450	0.207	0.217
SocS	0.001	0.001	0.001	0.000	0.003	0.003
Adult Female Density (AFD)	0.123	0.021	0.143	0.016	0.088	0.022
TSA x TD	0.058	0.067	0.086	0.095	0.032	0.033
TSA x SocS	0.001	0.001	0.004	0.004	0.003	0.003
TD x SocS	0.010	0.012	0.009	0.010	0.001	0.002
TSA x AFD	0.004	0.000	0.009	0.001	0.000	0.003
TD x AFD	0.007	0.003	0.023	0.011	0.052	0.013
SocS x AFD	0.002	0.000	0.001	0.000	0.009	0.003
TSA x TD x SocS	0.001	0.001	0.001	0.002	0.016	0.018
TSA x TD x AFD	0.003	0.000	0.009	0.000	0.011	0.002
TSA x SocS x AFD	0.001	0.001	0.002	0.002	0.001	0.003
TD x SocS x AFD	0.007	0.001	0.003	0.001	0.000	0.003
TSA x TD x SocS x AFD	0.001	0.001	0.002	0.002	0.007	0.003
Error	0.041	0.068	0.082	0.144	0.111	0.174

Tale 3.8. Results of pairwise Tukey's tests for the main effects in the ANOVAs for the six sets of analyses (a<b, a is not different from a,b, etc.). * indicates P of just over 0.05.

	Actual Adult Female Density			**Initial Adult Female Density**		
Blocks	**Trap Spatial Arrangement**	Mean	Significance	**Trap Spatial Arrangement**	Mean	Significance
16	Uniform	-0.609	a	Uniform	-0.597	a
	Random	-0.347	b	Random	-0.346	b
Blocks	**Trap Spatial Arrangement**	Mean	Significance	**Trap Spatial Arrangement**	Mean	Significance
9	Uniform	-0.603	a	Uniform	-0.595	a
	Random	-0.289	b	Random	-0.285	b
Blocks	**Trap Spatial Arrangement**	Mean	Significance	**Trap Spatial Arrangement**	Mean	Significance
4	Uniform	-0.644	a	Uniform	-0.635	a
	Random	-0.210	b	Random	-0.204	b
Blocks	**Trap Density**	Mean	Significance	**Trap Density**	Mean	Significance
16	0.05 Km^{-2}	-0.854	a	0.05 Km^{-2}	-0.842	a
	0.5 Km^{-2}	-0.308	b	0.5 Km^{-2}	-0.304	b
	1.0 Km^{-2}	-0.272	c	1.0 Km^{-2}	-0.270	c
Blocks	**Trap Density**	Mean	Significance	**Trap Density**	Mean	Significance
9	0.05 Km^{-2}	-0.733	a	0.05 Km^{-2}	-0.726	a
	0.5 Km^{-2}	-0.317	b	0.5 Km^{-2}	-0.312	b
	1.0 Km^{-2}	-0.288	b*	1.0 Km^{-2}	-0.282	b*
Blocks	**Trap Density**	Mean	Significance	**Trap Density**	Mean	Significance
4	0.05 Km^{-2}	-0.633	a	0.05 Km^{-2}	-0.620	a
	0.5 Km^{-2}	-0.332	b	0.5 Km^{-2}	-0.326	b
	1.0 Km^{-2}	-0.315	b	1.0 Km^{-2}	-0.313	b
Blocks	**Social Structure**	Mean	Significance	**Social Structure**	Mean	Significance
16	Groups within clans	-0.495	a	Groups within clans	-0.487	a
	Only clans	-0.476	a,b	Only clans	-0.465	a,b
	Individuals	-0.463	b,c	Individuals	-0.464	b,c
Blocks	**Social Structure**	Mean	Significance	**Social Structure**	Mean	Significance
9	Social Structure Not significant			Social Structure Not significant		
Blocks	**Social Structure**	Mean	Significance	**Social Structure**	Mean	Significance
4	Groups within clans	-0.434	a,b	Groups within clans	-0.426	a,b
	Only clans	-0.442	a	Only clans	-0.437	a
	Individuals	-0.404	b	Individuals	-0.395	b
Blocks	**Adult Female Density**	Mean	Significance	**Adult Female Density**	Mean	Significance
16	< 0.3 Individuals Km^{-2}	-0.599	a	0.2 Individuals Km^{-2}	-0.529	a
	>= 0.3 Individuals Km^{-2}	-0.357	b	0.4 Individuals Km^{-2}	-0.471	b
				0.8 Individuals Km^{-2}	-0.416	c
Blocks	**Adult Female Density**	Mean	Significance	**Adult Female Density**	Mean	Significance
9	< 0.3 Individuals Km^{-2}	-0.569	a	0.2 Individuals Km^{-2}	-0.493	a
	>= 0.3 Individuals Km^{-2}	-0.323	b	0.4 Individuals Km^{-2}	-0.425	b
				0.8 Individuals Km^{-2}	-0.403	b
Blocks	**Adult Female Density**	Mean	Significance	**Adult Female Density**	Mean	Significance
4	< 0.3 Individuals Km^{-2}	-0.522	a	0.2 Individuals Km^{-2}	-0.482	a
	>= 0.3 Individuals Km^{-2}	-0.332	b	0.4 Individuals Km^{-2}	-0.401	b
				0.8 Individuals Km^{-2}	-0.377	b

Table 3.9. Results of pairwise Tukey's tests for two of the two-way interactions in the ANOVAs for the six sets of analyses (a<b, a is not different from a,b, etc.).

	Actual Adult Female Density			**Initial Adult Female Density**		
Blocks	**Trap Spatial Arrangement x Trap Density**	Mean	Significance	**Trap Spatial Arrangement x Trap Density**	Mean	Significance
16	Uniform, 0.05 Km^{-2}	-0.869	a	Uniform, 0.05 Km^{-2}	-0.851	a
	Uniform, 0.5 Km^{-2}	-0.485	b	Uniform, 0.5 Km^{-2}	-0.473	b
	Uniform, 1.0 Km^{-2}	-0.474	b	Uniform, 1.0 Km^{-2}	-0.468	b
	Random, 0.05 Km^{-2}	-0.839	a	Random, 0.05 Km^{-2}	-0.833	a
	Random, 0.5 Km^{-2}	-0.132	c	Random, 0.5 Km^{-2}	-0.134	c
	Random, 1.0 Km^{-2}	-0.070	d	Random, 1.0 Km^{-2}	-0.072	d
Blocks	**Trap Spatial Arrangement x Trap Density**	Mean	Significance	**Trap Spatial Arrangement x Trap Density**	Mean	Significance
9	Uniform, 0.05 Km^{-2}	-0.756	a	Uniform, 0.05 Km^{-2}	-0.749	a
	Uniform, 0.5 Km^{-2}	-0.539	b	Uniform, 0.5 Km^{-2}	-0.531	b
	Uniform, 1.0 Km^{-2}	-0.514	b	Uniform, 1.0 Km^{-2}	-0.504	b
	Random, 0.05 Km^{-2}	-0.711	a	Random, 0.05 Km^{-2}	-0.703	a
	Random, 0.5 Km^{-2}	-0.095	c	Random, 0.5 Km^{-2}	-0.093	c
	Random, 1.0 Km^{-2}	-0.061	c	Random, 1.0 Km^{-2}	-0.061	c
Blocks	**Trap Spatial Arrangement x Trap Density**	Mean	Significance	**Trap Spatial Arrangement x Trap Density**	Mean	Significance
4	Uniform, 0.05 Km^{-2}	-0.771	a	Uniform x 0.05 /Km2	-0.759	a
	Uniform, 0.5 Km^{-2}	-0.602	b	Uniform x 0.5 /Km2	-0.592	b
	Uniform, 1.0 Km^{-2}	-0.558	b	Uniform x 1.0 /Km2	-0.554	b
	Random, 0.05 Km^{-2}	-0.495	c	Random x 0.05 /Km2	-0.482	c
	Random, 0.5 Km^{-2}	-0.062	d	Random x 0.5 /Km2	-0.06	d
	Random, 1.0 Km^{-2}	-0.072	d	Random x 1.0 /Km2	-0.071	d
Blocks	**Trap Spatial Arrangement x Social Structure**	Mean	Significance	**Trap Spatial Arrangement x Social Structure**	Mean	Significance
16	Not significant			Not significant		
Blocks	**Trap Spatial Arrangement x Social Structure**	Mean	Significance	**Trap Spatial Arrangement x Social Structure**	Mean	Significance
9	Uniform, groups within clans	-0.611	a,b	Uniform, groups within clans	-0.599	a
	Uniform, only clans	-0.628	a	Uniform, only clans	-0.618	a
	Uniform, individuals	-0.571	b	Uniform, individuals	-0.568	a
	Random, groups within clans	-0.300	c	Random, groups within clans	-0.297	b
	Random, only clans	-0.264	c	Random, only clans	-0.258	b
	Random, individuals	-0.303	c	Random, individuals	-0.301	b
Blocks	**Trap Spatial Arrangement x Social Structure**	Mean	Significance	**Trap Spatial Arrangement x Social Structure**	Mean	Significance
4	Uniform, groups within clans	-0.657	a	Uniform, groups within clans	-0.650	a
	Uniform, only clans	-0.676	a	Uniform, only clans	-0.670	a
	Uniform, individuals	-0.598	b	Uniform, individuals	-0.586	b
	Random, groups within clans	-0.211	c	Random, groups within clans	-0.203	c
	Random, only clans	-0.209	c	Random, only clans	-0.205	c
	Random, individuals	-0.210	c	Random, individuals	-0.205	c

Table 3.10. Results of pairwise Tukey’s tests for trap density x adult female density interaction in the ANOVAs for the six sets of analyses (a<b, a is not different from a,b, etc.).

	Actual Adult Female Density			**Initial Adult Female Density**		
Blocks	**Trap Density x Adult Female Density**	Mean	Significance	**Trap Density x Adult Female Density**	Mean	Significance
16	0.05 Km^{-2}, <0.3 Individuals Km^{-2}	-0.952	a	0.05 Km^{-2}, 0.2 Individuals Km^{-2}	-0.923	a
	0.05 Km^{-2}, $\geq$0.3 Individuals Km^{-2}	-0.756	b	0.05 Km^{-2}, 0.4 Individuals Km^{-2}	-0.848	b
	0.5 Km^{-2}, <0.3 Individuals Km^{-2}	-0.471	c	0.05 Km^{-2}, 0.8 Individuals Km^{-2}	-0.755	c
	0.5 Km^{-2}, $\geq$0.3 Individuals Km^{-2}	-0.146	d	0.5 Km^{-2}, 0.2 Individuals Km^{-2}	-0.361	d
	1 Km^{-2}, <0.3 Individuals Km^{-2}	-0.374	e	0.5 Km^{-2}, 0.4 Individuals Km^{-2}	-0.299	e, f
	1 Km^{-2}, $\geq$0.3 Individuals Km^{-2}	-0.170	d	0.5 Km^{-2}, 0.8 Individuals Km^{-2}	-0.252	e,g
				1 Km^{-2}, 0.2 Individuals Km^{-2}	-0.302	f,h
				1 Km^{-2}, 0.4 Individuals Km^{-2}	-0.266	e,g,h
				1 Km^{-2}, 0.8 Individuals Km^{-2}	-0.241	g
Blocks	**Trap Density x Adult Female Density**	Mean	Significance	**Trap Density x Adult Female Density**	Mean	Significance
9	0.05 Km^{-2}, <0.3 Individuals Km^{-2}	-0.924	a	0.05 Km^{-2}, 0.2 Individuals Km^{-2}	-0.821	a
	0.05 Km^{-2}, >=0.3 Individuals Km^{-2}	-0.543	b	0.05 Km^{-2}, 0.4 Individuals Km^{-2}	-0.729	b
	0.5 Km^{-2}, <0.3 Individuals Km^{-2}	-0.421	c	0.05 Km^{-2}, 0.8 Individuals Km^{-2}	-0.629	c
	0.5 Km^{-2}, >=0.3 Individuals Km^{-2}	-0.213	d	0.5 Km^{-2}, 0.2 Individuals Km^{-2}	-0.356	d
	1 Km^{-2}, <0.3 Individuals Km^{-2}	-0.363	e	0.5 Km^{-2}, 0.4 Individuals Km^{-2}	-0.285	e
	1 Km^{-2}, >=0.3 Individuals Km^{-2}	-0.213	d	0.5 Km^{-2}, 0.8 Individuals Km^{-2}	-0.294	d, e
				1 Km^{-2}, 0.2 Individuals Km^{-2}	-0.302	d, e
				1 Km^{-2}, 0.4 Individuals Km^{-2}	-0.260	e
				1 Km^{-2}, 0.8 Individuals Km^{-2}	-0.285	e
Blocks	**Trap Density x Adult Female Density**	Mean	Significance	**Trap Density x Adult Female Density**	Mean	Significance
4	0.05 Km^{-2}, <0.3 Individuals Km^{-2}	-0.832	a	0.05 Km^{-2}, 0.2 Individuals Km^{-2}	-0.739	a
	0.05 Km^{-2}, >=0.3 Individuals Km^{-2}	-0.434	b	0.05 Km^{-2}, 0.4 Individuals Km^{-2}	-0.606	b
	0.5 Km^{-2}, <0.3 Individuals Km^{-2}	-0.376	b,c	0.05 Km^{-2}, 0.8 Individuals Km^{-2}	-0.515	c
	0.5 Km^{-2}, >=0.3 Individuals Km^{-2}	-0.288	d	0.5 Km^{-2}, 0.2 Individuals Km^{-2}	-0.360	d
	1 Km^{-2}, <0.3 Individuals Km^{-2}	-0.358	c	0.5 Km^{-2}, 0.4 Individuals Km^{-2}	-0.300	d
	1 Km^{-2}, >=0.3 Individuals Km^{-2}	-0.273	d	0.5 Km^{-2}, 0.8 Individuals Km^{-2}	-0.318	d
				1 Km^{-2}, 0.2 Individuals Km^{-2}	-0.346	d
				1 Km^{-2}, 0.4 Individuals Km^{-2}	-0.296	d
				1 Km^{-2}, 0.8 Individuals Km^{-2}	-0.296	d

Table 3.11. Results of pairwise Tukey's tests for two of the two-way interactions in the ANOVAs for the six sets of analyses (a<b, a is not different from a,b, etc.).

	Actual Adult Female Density			**Initial Adult Female Density**		
Blocks	**Trap Density x Social Structure**	Mean	Significance	**Trap Density x Social Structure**	Mean	Significance
16	0.05 Km^{-2}, groups within clans	-0.841	a	0.05 Km^{-2}, groups within clans	-0.831	a
	0.05 Km^{-2}, only clans	-0.816	a	0.05 Km^{-2}, only clans	-0.796	a
	0.05 Km^{-2}, individuals	-0.904	b	0.05 Km^{-2}, individuals	-0.900	b
	0.5 Km^{-2}, groups within clans	-0.356	c	0.5 Km^{-2}, groups within clans	-0.343	c
	0.5 Km^{-2}, only clans	-0.310	c,d	0.5 Km^{-2}, only clans	-0.303	c,d
	0.5 Km^{-2}, individuals	-0.259	e,f	0.5 Km^{-2}, individuals	-0.265	d,e
	1 Km^{-2}, groups within clans	-0.290	d,e	1 Km^{-2}, groups within clans	-0.285	d
	1 Km^{-2}, only clans	-0.301	d,e	1 Km^{-2}, only clans	-0.298	c,d
	1 Km^{-2}, individuals	-0.225	f	1 Km^{-2}, individuals	-0.226	e
Blocks	**Trap Density x Social Structure**	Mean	Significance	**Trap Density x Social Structure**	Mean	Significance
9	0.05 Km^{-2}, groups within clans	-0.722	a,b	0.05 Km^{-2}, groups within clans	-0.717	a,b
	0.05 Km^{-2}, only clans	-0.694	b	0.05 Km^{-2}, only clans	-0.683	a
	0.05 Km^{-2}, individuals	-0.784	a	0.05 Km^{-2}, individuals	-0.778	b
	0.5 Km^{-2}, groups within clans	-0.327	c	0.5 Km^{-2}, groups within clans	-0.317	c
	0.5 Km^{-2}, only clans	-0.346	c	0.5 Km^{-2}, only clans	-0.336	c
	0.5 Km^{-2}, individuals	-0.278	c,d	0.5 Km^{-2}, individuals	-0.283	c,d
	1 Km^{-2}, groups within clans	-0.316	c	1 Km^{-2}, groups within clans	-0.310	c,d
	1 Km^{-2}, only clans	-0.299	c,d	1 Km^{-2}, only clans	-0.295	c,d
	1 Km^{-2}, individuals	-0.248	d	1 Km^{-2}, individuals	-0.242	d
Blocks	**Trap Density x Social Structure**	Mean	Significance	**Trap Density x Social Structure**	Mean	Significance
4	Not significant			Not significant		
Blocks	**Social Structure x Adult Female Density**	Mean	Significance	**Social Structure x Adult Female Density**	Mean	Significance
16	Groups in clans, < 0.3 Ind. Km^{-2}	-0.614	a			
	Groups in clans, >= 0.3 Ind. Km^{-2}	-0.377	b	Not significant		
	Only clans, < 0.3 Ind. Km^{-2}	-0.578	a			
	Only clans, >= 0.3 Ind. Km^{-2}	-0.374	b			
	Individuals, < 0.3 Ind. Km^{-2}	-0.605	a			
	Individuals, >= 0.3 Ind. Km^{-2}	-0.321	c			
Blocks	**Social Structure x Adult Female Density**	Mean	Significance	**Social Structure x Adult Female Density**	Mean	Significance
9	Not significant			Not significant		
Blocks	**Social Structure x Adult Female Density**	Mean	Significance	**Social Structure x Adult Female Density**	Mean	Significance
4	Groups in clans, < 0.3 Ind. Km^{-2}	-0.510	a			
	Groups in clans, >= 0.3 Ind. Km^{-2}	-0.359	b	Not significant		
	Only clans, < 0.3 Ind. Km^{-2}	-0.516	a			
	Only clans, >= 0.3 Ind. Km^{-2}	-0.369	b			
	Individuals, < 0.3 Ind. Km^{-2}	-0.541	a			
	Individuals, >= 0.3 Ind. Km^{-2}	-0.267	c			

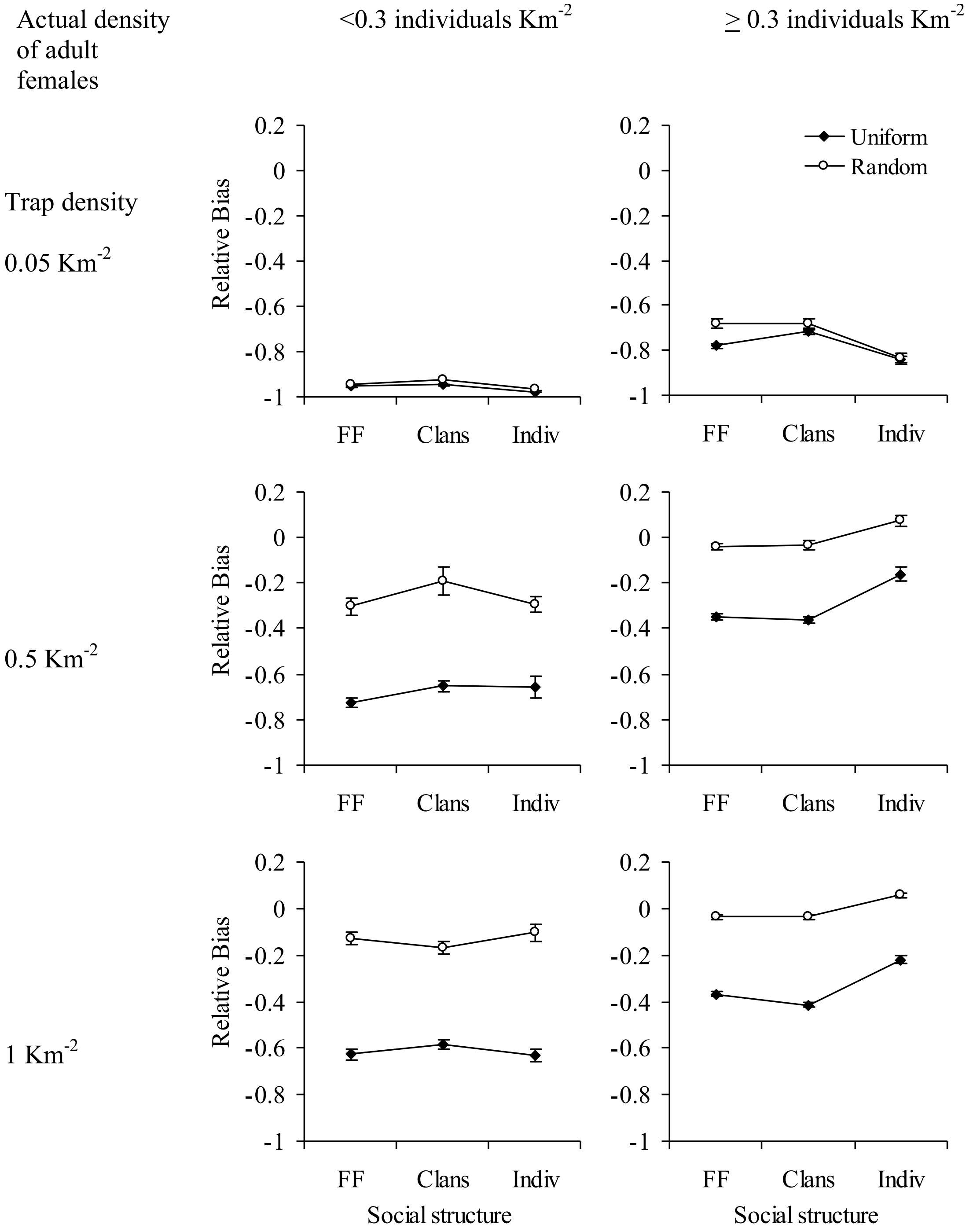

Figure 3.1. Results from POPAN for the sampling scale of 16 blocks: relative bias (± SE) for different social structures (FF: fission-fusion, groups within clans; Clans: only clans, Indiv: non-associating individuals) for different combinations of actual adult female density and trap density for uniform and random spatial arrangements of traps.

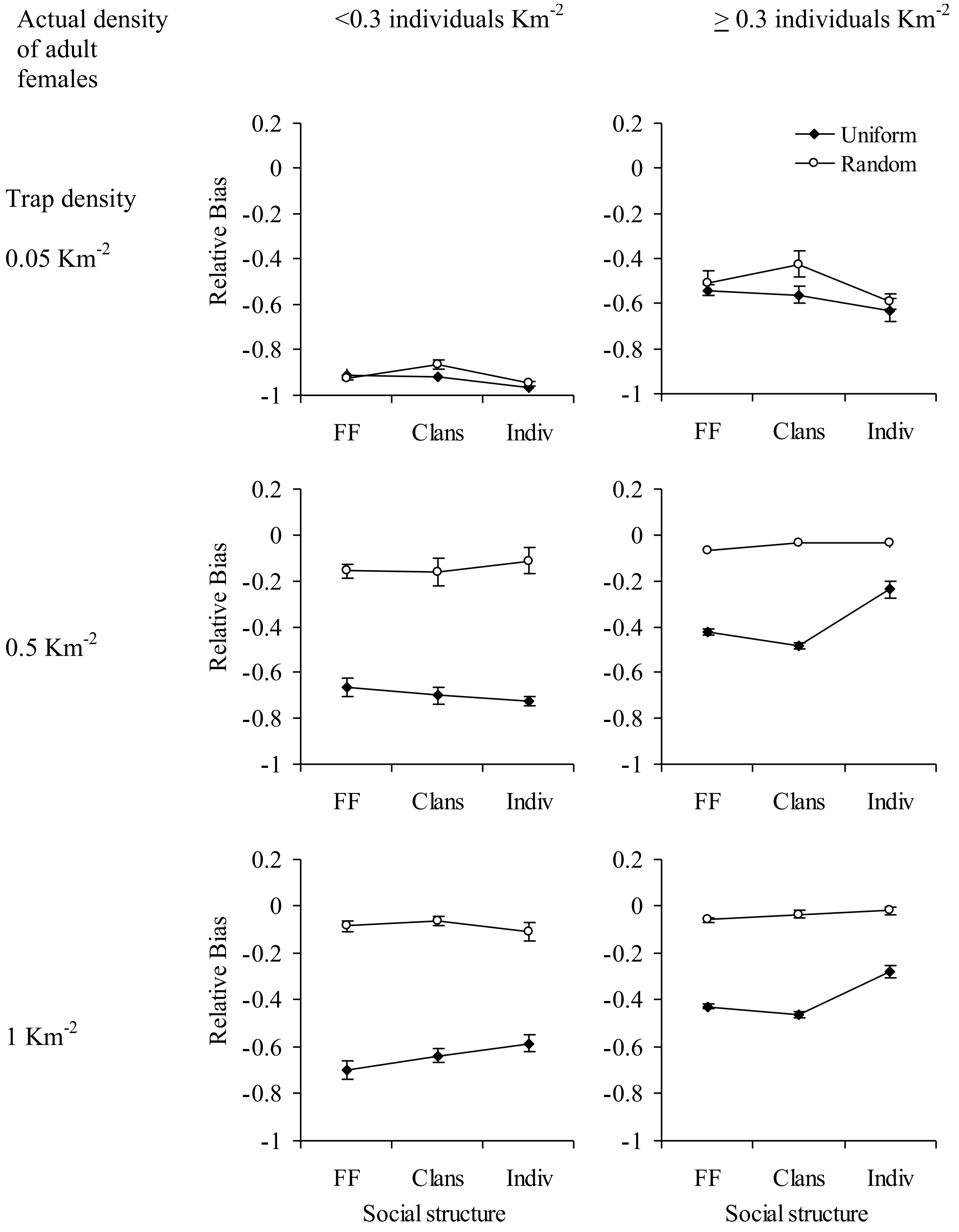

Figure 3.2. Results from POPAN for the sampling scale of nine blocks: relative bias (± SE) for different social structures (FF: fission-fusion, groups within clans; Clans: only clans, Indiv: non-associating individuals) for different combinations of actual adult female density and trap density for uniform and random spatial arrangements of traps.

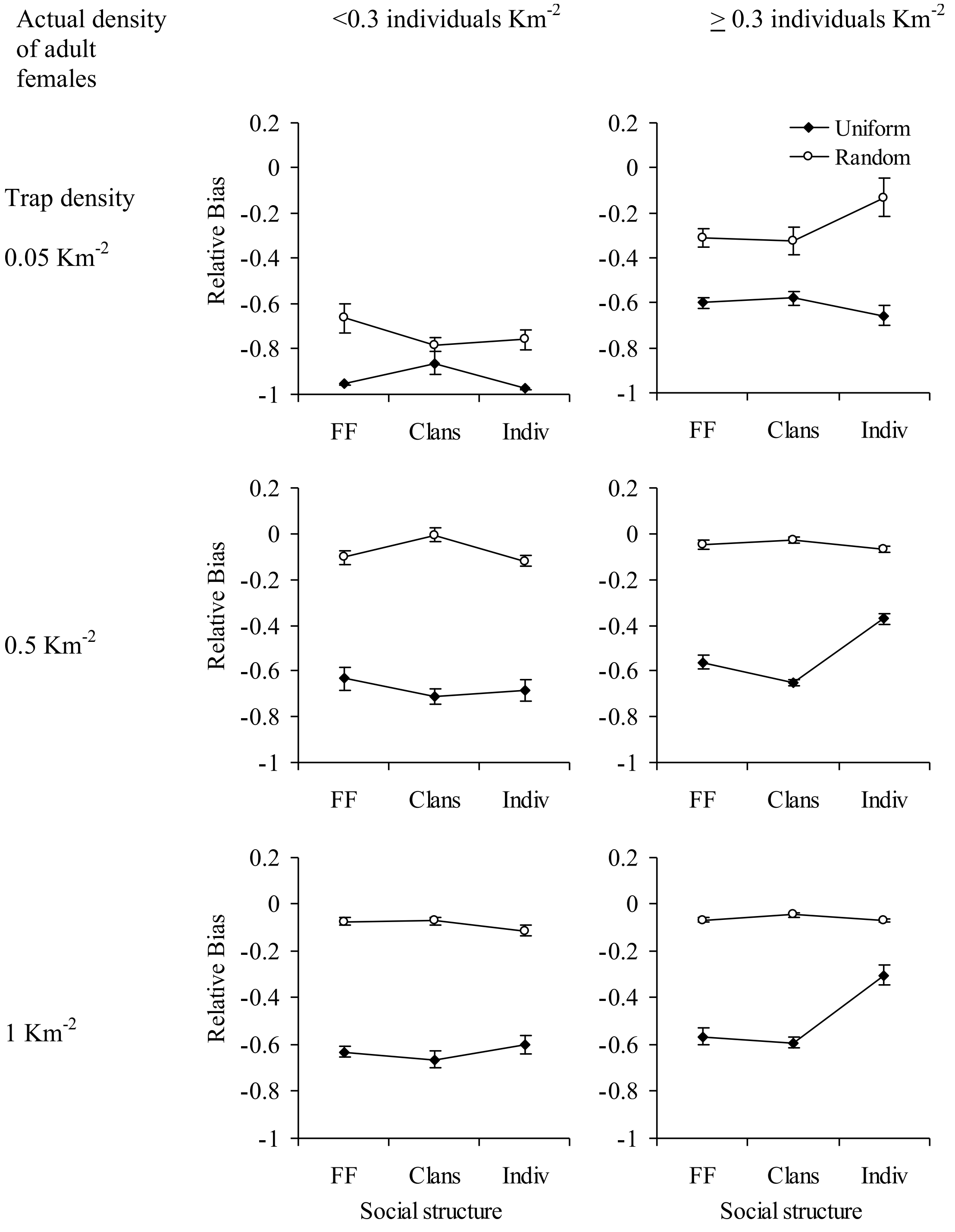

Figure 3.3. Results from POPAN for the sampling scale of four blocks: relative bias (± SE) for different social structures (FF: fission-fusion, groups within clans; Clans: only clans, Indiv: non-associating individuals) for different combinations of actual adult female density and trap density for uniform and random spatial arrangements of traps.

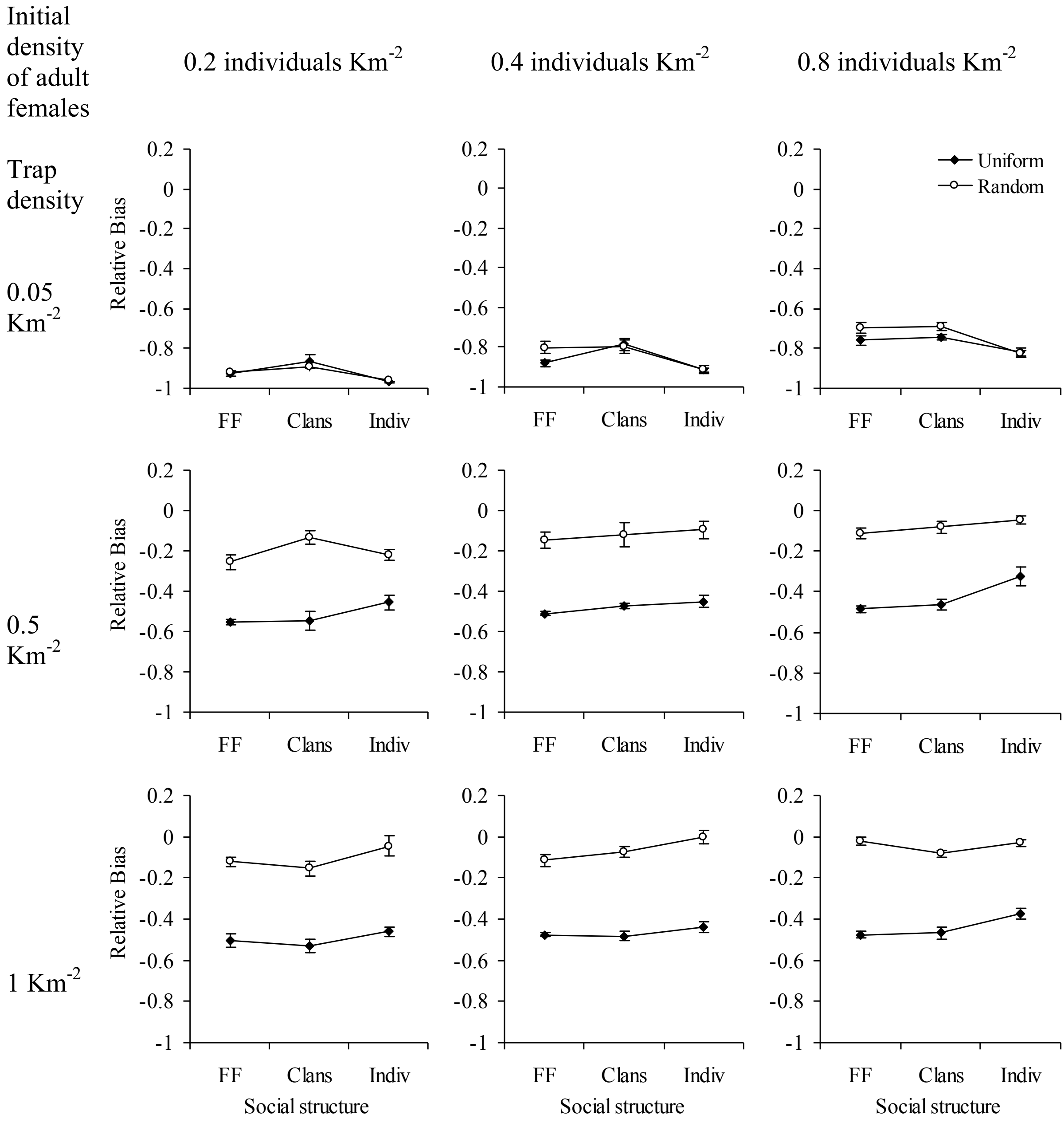

Figure 3.4. Results from POPAN for the sampling scale of 16 blocks: relative bias (± SE) for different social structures (FF: fission-fusion, groups within clans; Clans: only clans, Indiv: non-associating individuals) for different combinations of initial adult female density and trap density for uniform and random spatial arrangements of traps.

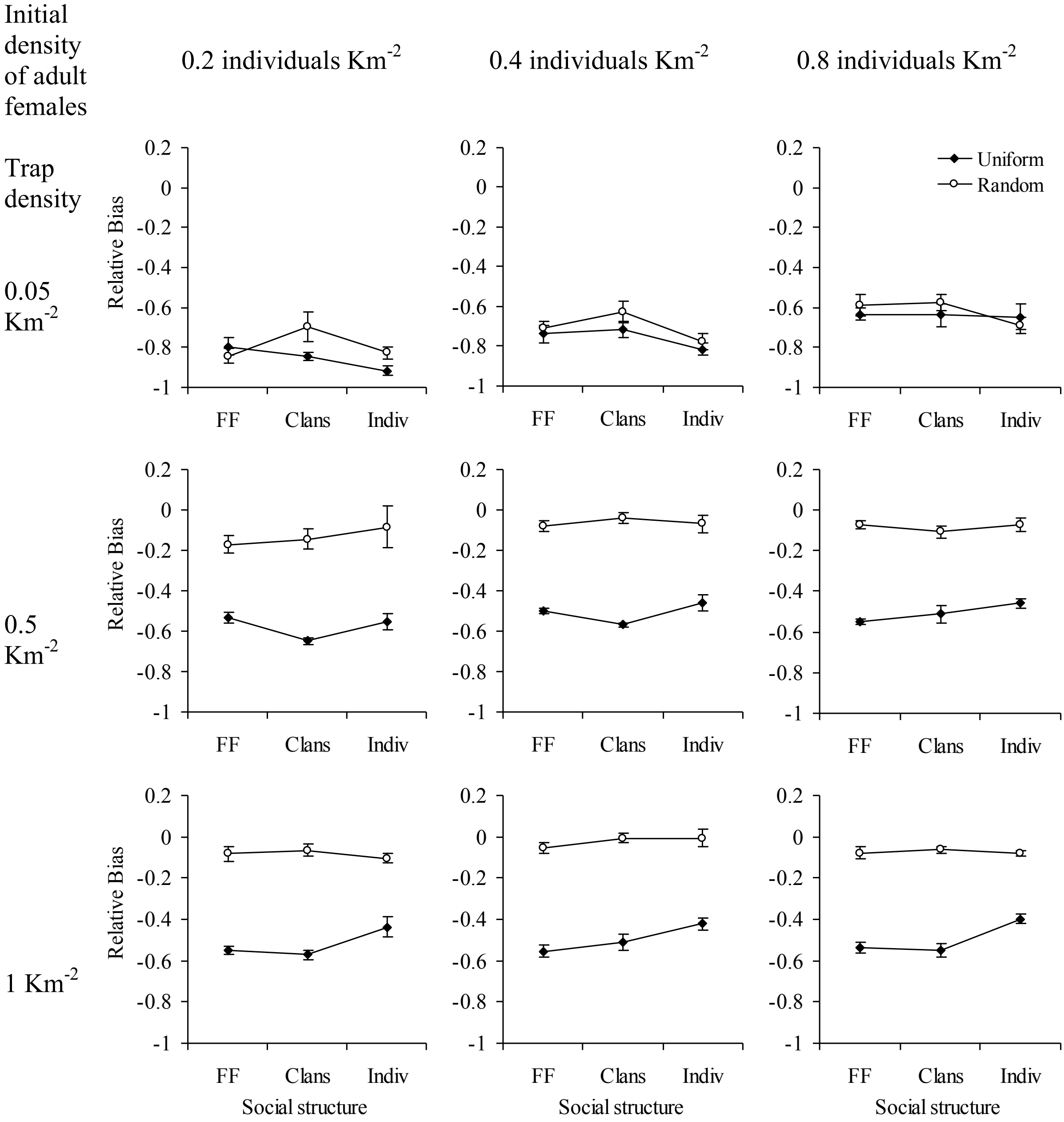

Figure 3.5. Results from POPAN for the sampling scale of nine blocks: relative bias (± SE) for different social structures (FF: fission-fusion, groups within clans; Clans: only clans, Indiv: non-associating individuals) for different combinations of initial adult female density and trap density for uniform and random spatial arrangements of traps.

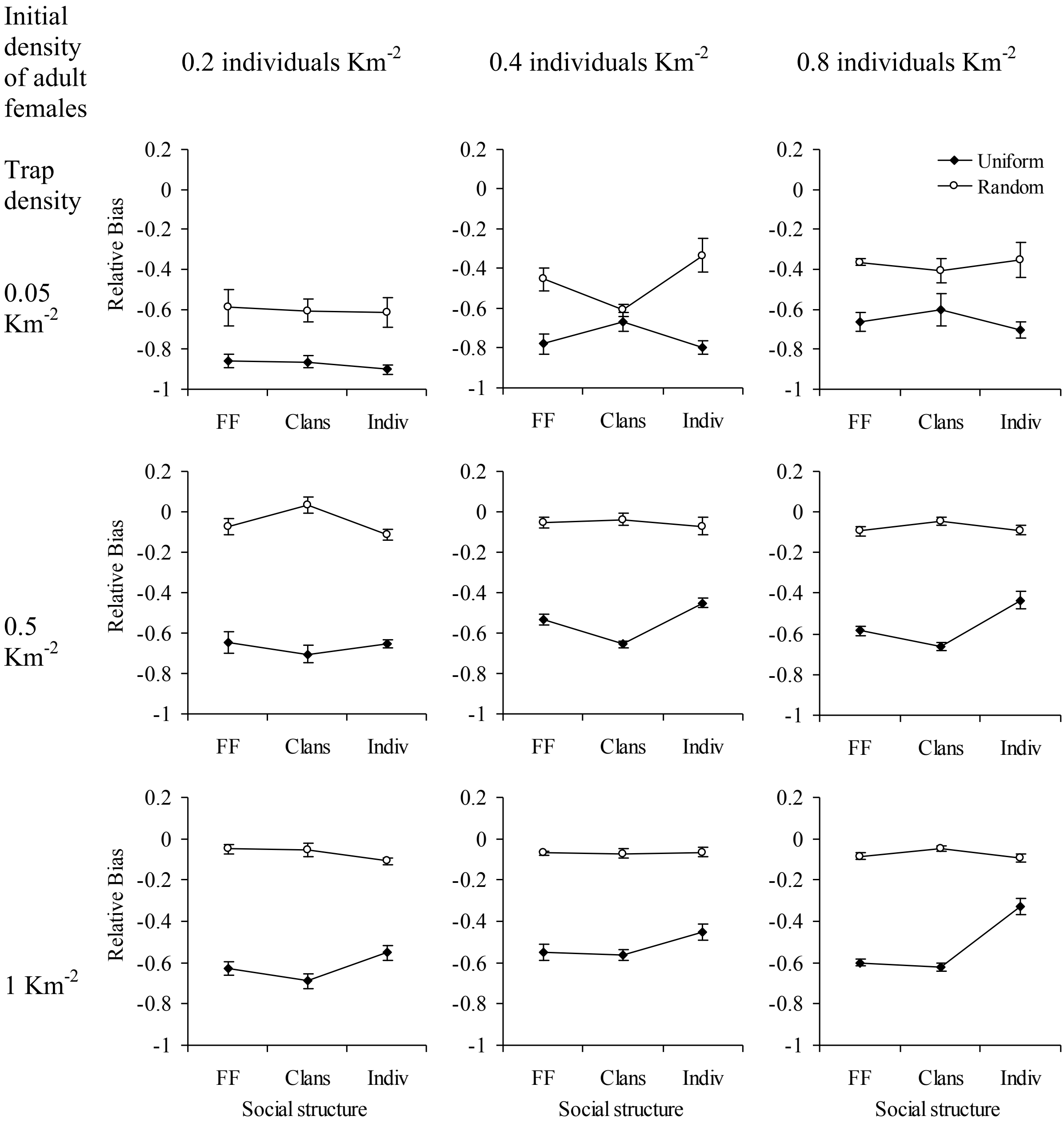

Figure 3.6. Results from POPAN for the sampling scale of four blocks: relative bias (± SE) for different social structures (FF: fission-fusion, groups within clans; Clans: only clans, Indiv: non-associating individuals) for different combinations of initial adult female density and trap density for uniform and random spatial arrangements of traps.

3.2 Discussion

The POPAN estimator of superpopulation size performed satisfactorily when trap density was high and the trap arrangement was random, although it almost always gave underestimates of superpopulation size. Underestimates are expected as a result of individual heterogeneity in capture rates, which would lead to a situation in which individuals with higher capture probabilities get marked at a higher rate than other individuals early in the study and, subsequently, the proportion of these marked individuals amongst the individuals captured during later occasions becomes an overestimate of the actual proportion of marked individuals in the total population (as unmarked individuals are captured at a lower rate than marked individuals) (Pollock *et al.* 1990). The overestimate of the proportion of marked individuals leads to underestimates of superpopulation sizes. Trap density (or trapping effort) is known to be very important in mark-recapture studies. Low trapping effort could result in ‘holes’, i.e., a sub-area in the entire study area that experiences no trapping effort at all, thereby reducing capture probabilities in general and even rendering null capture probabilities for some individuals (Williams *et al.* 2002, Karanth *et al.* 2011). Low trapping effort will, therefore, lead to biased estimates (Williams *et al.* 2002, Karanth *et al.* 2011). The better performance of random trap arrangement showed that it is better to ensure complete sampling of a localized area rather than spreading the trapping effort evenly over the entire area. The former strategy is likely to work for a wide-ranging species such as the Asian elephant, but possibly not for species with much smaller home ranges, because randomly placed traps are more likely than uniformly placed traps to miss out certain home ranges, given a particular trap density. It is possible that random traps performed better than uniform traps in my simulations because movement in the simulations was also random. Whether random traps also perform well when other kinds of movement patterns, such as directed movement, are modelled remains to be seen.

The combination of high trap density and random trap arrangement was not affected by the underlying social structure of the population, and social structure, in general, explained a very small amount of variation in relative bias overall. However, social structure did have a significant main effect and several significant interactions with other factors, primarily because of variations in bias when uniformly placed traps were used. If low trap densities (which tend to perform poorly anyway) were excluded, the difference between uniformly placed and randomly placed traps was smaller for non-associating individuals compared to groups within clans and only clans. Therefore, it would be more important to use randomly placed rather than uniformly placed traps if the study species showed group structure than if it was non-associating.

The sampling scale of four blocks performed better than the other two sampling scales as expected (see Williams *et al.* 2002). This was probably due to the perimeter-to-area ratio being the least for the four blocks sampling scale, which results in a smaller proportion of individuals being near the edge and, therefore, lower individual heterogeneity in capture probabilities due to temporary migration. Ideally, mark-recapture estimators should give unbiased estimates of population size for any density of individuals, however, the density of individuals becomes a factor in unbiased estimation of population size when sampling effort is very low.

Overall, the above results suggest that ensuring a relatively high sampling effort should solve the problem of dependence of captures between individuals as very similar mean relative biases were obtained for all three social structures when trap density was high. Trap arrangement in uniform grids should be avoided. In this study the random trap arrangement worked very well, although it has been suggested that traps should be placed at location frequently visited by animals so as to maximize capture probabilities (Karanth *et al*. 2011). However, non-random movement needs to be modelled in the future to check the efficacy of the random trap placement.

CHAPTER 4: RESULTS AND DISCUSSION: ROBUST DESIGN WITH HETEROGENEITY

4.1 Results

Analyses of variance (ANOVAs) on relative bias, averaged across blocks, for each replicate run of simulations were performed separately for data from each spatial scale of sampling (i.e., 16 blocks, nine blocks and four blocks), considering initial adult female density (0.2, 0.4 and 0.8 individuals Km^{-2}) as the factor adult female density. The other factors included in each analysis were spatial trap arrangement (uniform and random), trap density (0.05, 0.5 and 1.0 traps Km^{-2}), and social structure (fission-fusion, fixed clans, and non-associating individuals). Thus, three four-factor completely randomized ANOVAs were done for the data obtained from Robust Design analysis of the simulated data sets, modelling individual heterogeneity as two mixture of capture probabilities. The results of the ANOVAs are summarized in Tables 4.1-4.3. Problems in convergence of the maximum likelihood estimation of population parameters, including population size, in MARK (White and Burnham 1999) (used through RMark (Laake 2013)) led to incomplete ANOVA designs when actual density of females in blocks was considered as a factor. The analyses considering initial females density as a factor had unequal sample sizes due to similar reasons.

Overall, population sizes were greatly underestimated by the estimator using Robust Design with heterogeneity. The pattern of effects of the four factors on relative bias of the Robust Design with heterogeneity estimator was very similar across analyses considering the three different sampling scales (compare respective panels across Figures 4.1-4.3). Spatial trap arrangement and trap density were able to explain the majority of the variation in relative bias, consistently contributing about 80-85% of the total sum of squares (TSS) across all three ANOVAs (Table 4.4). The spatial trap arrangement × trap density interaction accounted for a further 10% or so of the variation in relative bias across all analyses (Table 4.4).

The main effects of spatial trap arrangement and trap density, and the spatial trap arrangement x trap density interaction, were highly significant ($P<0.001$ for all) in all three ANOVAs (Tables 4.1-4.3). The random trap arrangement yielded, on average, about 11 to 22% lower absolute values of relative bias than the uniform trap arrangement (see Figures 4.1-4.3, Table 4.5). In general, absolute values of relative bias were largest at the lowest trap density (0.05 Km^{-2}) (Figures 4.1-4.3, Table 4.6). However, absolute values of relative bias decreased monotonically with increasing trap density only in the case of 4 blocks, whereas for sampling scales of 16 and nine blocks, trap densities of 0.5 and 1 traps Km^{-2} yielded smaller absolute values of relative bias than the 0.05 traps Km^{-2} trap density, but did not differ significantly amongst themselves (Table 4.6). There was no difference in relative bias between uniform and random trap arrangement when trap density was 0.05 traps Km^{-2}, except when the sampling scale was four blocks, whereas the differences in relative bias between uniform and random trap arrangement were large and significant when the sampling scale was either 16 or nine blocks (see Figures 4.1-4.3, Table 4.5).

Both the main effect of social structure, as well as the trap density x social structure interaction, were also highly significant ($P<0.001$ for all) in all three ANOVAs (Tables 4.1-4.3). Overall, when averaged across all levels of the other three factors, the social structure representing non-associating individuals consistently yielded the least absolute values of relative bias, whereas the relative biases for the social structures representing fission-fusion societies and just clans were significantly higher than those for non-associating individuals but did not differ significantly between themselves (Table 4.5). Thus, at all three spatial scales of sampling, incorporating social structure in the form of either just clans or groups within clans resulted in greater underestimation of population size than the case considering just non-associating individuals (i.e., no social stucture), when using the Robust Design estimator with heterogeneity. There were no significant differences in relative bias between the three social structures when trap density was the lowest (0.05 Km^{-2}), whereas the non-associating individuals social structure yielded significantly lower absolute values of relative bias than the other two social structures (i.e. fission-fusion societies and just clans) for the two higher trap densities of 0.5 and 1 trap Km^{-2} (Figures 4.1-4.3; Table 4.7). Moreover, absolute values of relative bias were lower, on an average, for all three social structures when trap densities were either 0.5 or 1 trap Km^{-2} than in the case of 0.05 traps Km^{-2} (Figures 4.1-4.3, Table 4.7).

Initial adult female density showed a significant ($P<0.025$) main effect in only two of the ANOVAs: spatial sampling scale corresponding to either 16 or nine blocks (Tables 4.1-4.3). In both of these cases, the trend was for absolute value of relative bias to be slightly reduced at higher initial adult female density (Figures 4.1, 4.2; Table 4.5). The only significant two-way interaction involving initial adult female density was seen in the spatial sampling scale of four blocks, in which there was a highly significant ($P<0.01$) trap spatial arrangement x initial adult female density interaction (Table 4.3, Table 4.7). This interaction appeared to be the result of an apparent non-parellellism, driven largely by the results from the lowest trap density of 0.05 Km^{-2} (Figure 4.3, top three panels), in responses of relative bias to increasing initial adult female density within each of the two trap spatial arrangements, uniform or random. In the uniform trap spatial arrangement, the least absolute value of relative bias (-0.895) was for the intermediate initial adult female density of 0.4 individuals Km^{-2}, whereas in the random trap spatial arrangement, the least absolute value of relative bias (-0.676) was for the highest initial adult female density of 0.8 individuals Km^{-2} (Table 4.7). However, none of the pairwise differences within each trap spatial arrangement were significant using Tukey's HSD test (Table 4.7); this might be due to the reduction of statistical power in the HSD test due to unequal sample sizes.

Other than the significant main effects and two-way interactions discussed above, only two three-way interactions were significant across the three ANOVAs with different spatial scales of sampling (Tables 4.2, 4.3). In both cases, however, there were no clear and generalizable trends apparent; the interactions seemed to be driven primarily by haphazardly varying patterns of relative bias values across different combinations of factor levels (Figures 4.2, 4.3). In the case of sampling spatial scale represented by nine blocks, the trap density x social structure x initial adult female density interaction was highly significant ($P<0.01$: Table 4.2). Within the lowest trap density (0.05 Km^{-2}), none of the nine combinations of social structure x initial adult female density differed significantly among themselves in relative bias. Across the two higher trap densities (0.5 and 1 Km^{-2}), some combinations of social structure x initial adult female density did differ among themselves in relative bias, but there was no overall pattern to these differences (Figure 4.2; Table 4.8). In the case of sampling spatial scale represented by four blocks, the trap spatial arrangement x trap density x social structure interaction was highly significant ($P<0.01$: Table 4.3). Within the uniform trap spatial arrangement, none of the nine combinations of trap density x social structure differed significantly among themselves in relative bias. Across the random trap spatial arrangement, some combinations of trap density x social structure did differ among themselves in relative bias, but there was no overall pattern to these differences (Figure 4.3; Table 4.9).

4.2 Discussion

The overall pattern of effects of different factors and interactions on absolute values of relative bias for the Robust Design estimator with individual heterogeneity modelled as two mixtures of capture probabilities was qualitatively similar to that obtained for the POPAN estimator (see Chapter 3). However, compared to the results from the POPAN estimator, the absolute values of relative bias obtained with the Robust Design estimator are considerably higher and, indeed, never fall below about -0.5 for any combination of factor levels (Figures 4.1-4.3). There might be two contributing factors to this greater bias with the Robust Design estimator. First, there were problems with convergence of the maximum likelihood estimation algorithm using MARK (through RMark), and some estimates may therefore be artifactually low due to faulty estimates of other population parameters like survival and capture probability. Second, and perhaps more important, is the possible violation of the closure assumption for Robust Design's primary intervals. I had set the primary interval to be seven days long but, during this period, individuals in the simulation could have entered or exited the study area. Any such movement would result in lowered capture probabilities which can lead to an underestimate of population size, especially if certain individuals leave the population without ever getting sighted (Otis *et al.* 1978, Kendall 1999, Williams *et al.* 2002).

With regard to the broad pattern of how trap spatial arrangement, trap density, social structure and initial adult female density affect relative bias, the results for the Robust Design estimator with individual heterogeneity are qualitatively similar to those seen for the POPAN estimator. Overall, it was observed that trap density and trap spatial arrangement were the leading determinants of bias in the population size estimates, as in the case of the POPAN estimator. Relatively high initial adult female density also resulted in small decreases in relative bias, similar in direction but much lower in magnitude to those seen in the case of the POPAN estimator. It was expected that higher trap densities will lead to lower absolute values of relative bias (Otis *et al*. 1978, Williams *et al*. 2002), and this trend was clear in my results. On the other hand, random trap arrangement yielding relatively more unbiased estimates, as in my results, is not immediately intuitive, although Karanth *et al.* (2011) have suggested that uniform trap arrangements do not give very robust estimates of population size. Essentially, for the uniform trap arrangement, no particular region of the block is intensively covered, increasing the probability that more individuals will remain in 'holes' (un-sampled area) throughout primary occasions. The convex-hull areas of groups of individuals in my simulations were usually of the order of 2-5 Km^2 across both fixed-clans and fission-fusion social structures, whereas the capture range of a trap was only set to be 100 m in radius ($\pi \times 10^{-2}$ Km^2). Thus, in the case of uniform trap arrangement in my simulations, a single trap cannot capture all individuals of group with such convex-hull areas. However, in the case of random trap arrangement, there is a possibility of aggregation of traps close to each other. Such an arrangement would ensure capture of complete groups. In principle, it is advisable to place traps at locations which are known to be visited frequently by individuals (Karanth *et al.* 2011), but in my simulations the movement of individuals and groups is random. This is probably why the random trap arrangement gives less biased estimates of population size using data from these simulations. As expected, the non-associating individuals yielded lower absolute values of relative bias, though only in the case of moderate to high trapping intensities, as the assumption of independence of captures is not violated in this case. In other words, the presence of social structure of either the fission-fusion society type or the fixed clans type is likely to yield large underestimates of population size using the Robust Design estimator with individual heterogeneity because when animals move in groups, or groups-within-groups, the assumption of independence of individual capture events is clearly violated. The Robust Design estimator with individual heterogeneity is, therefore, not advisable for use with species exhibiting social structure, leading to coordinated movement of groups of individuals. Thus, it would probably be advisable to use open population models, like the POPAN model (Schwarz and Arnason 1996), or the open Robust Design (Schwarz and Stobo 1997) while sampling at high intensities with traps located at either animal hot-spots or in a random arrangement.

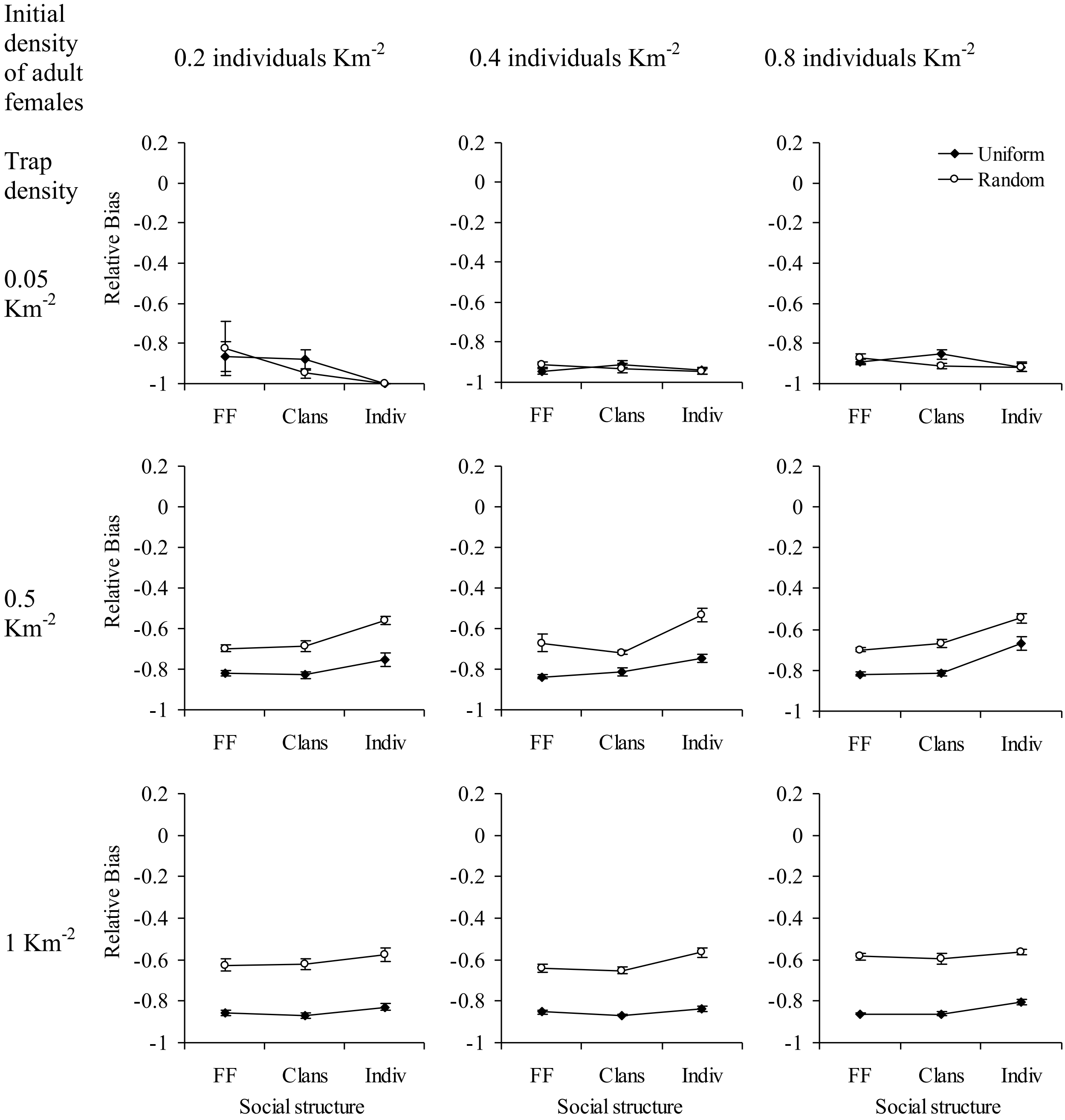

Figure 4.1. Results from Robust Design with heterogeneity for the sampling scale of 16 blocks: relative bias (± SE) for different social structures (FF: fission-fusion, groups within clans; Clans: only clans, Indiv: non-associating individuals) for different combinations of initial adult female density and trap density for uniform and random spatial arrangements of traps.

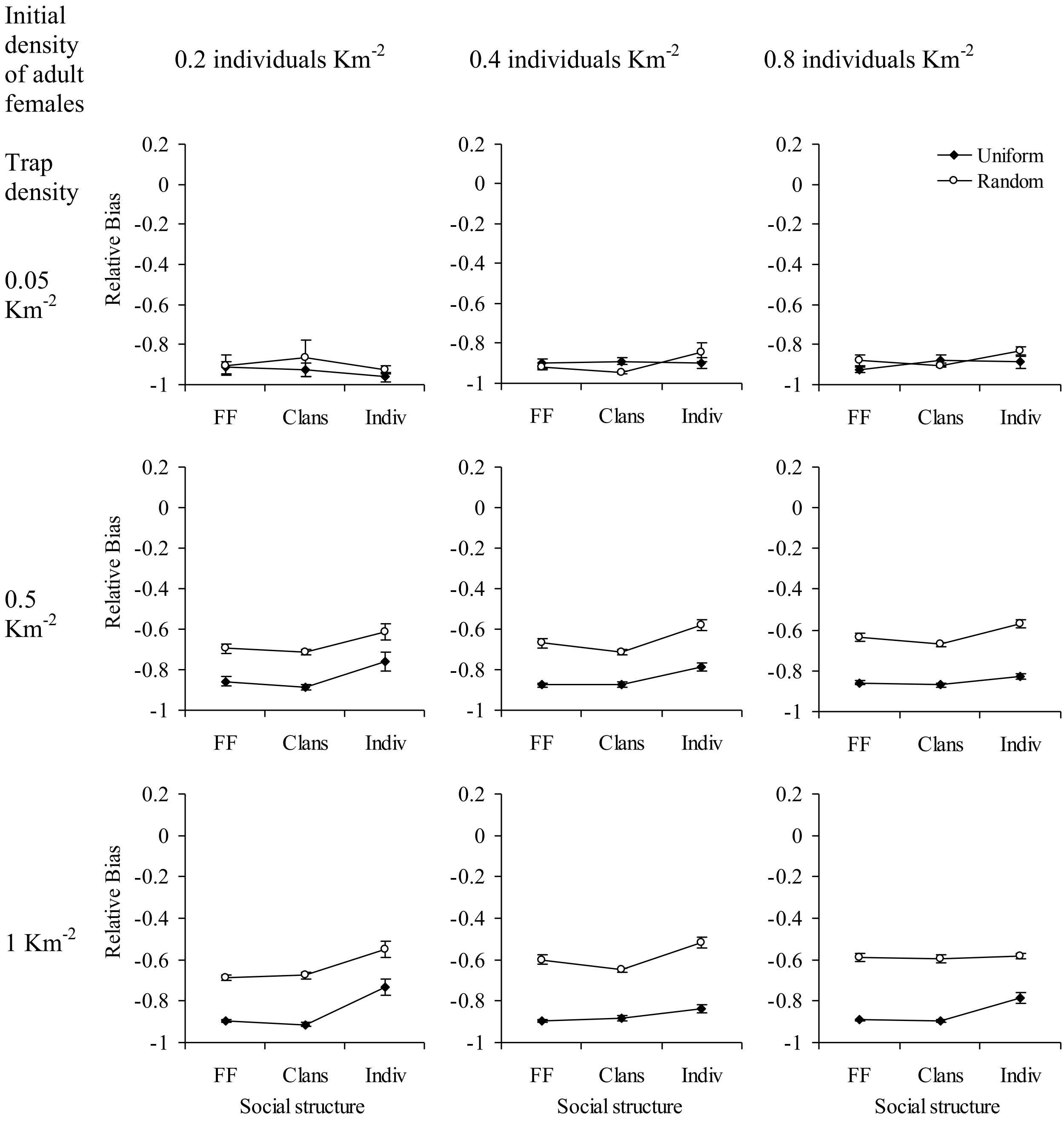

Figure 4.2. Results from Robust Design with heterogeneity for the sampling scale of nine blocks: relative bias (± SE) for different social structures (FF: fission-fusion, groups within clans; Clans: only clans, Indiv: non-associating individuals) for different combinations of initial adult female density and trap density for uniform and random spatial arrangements of traps.

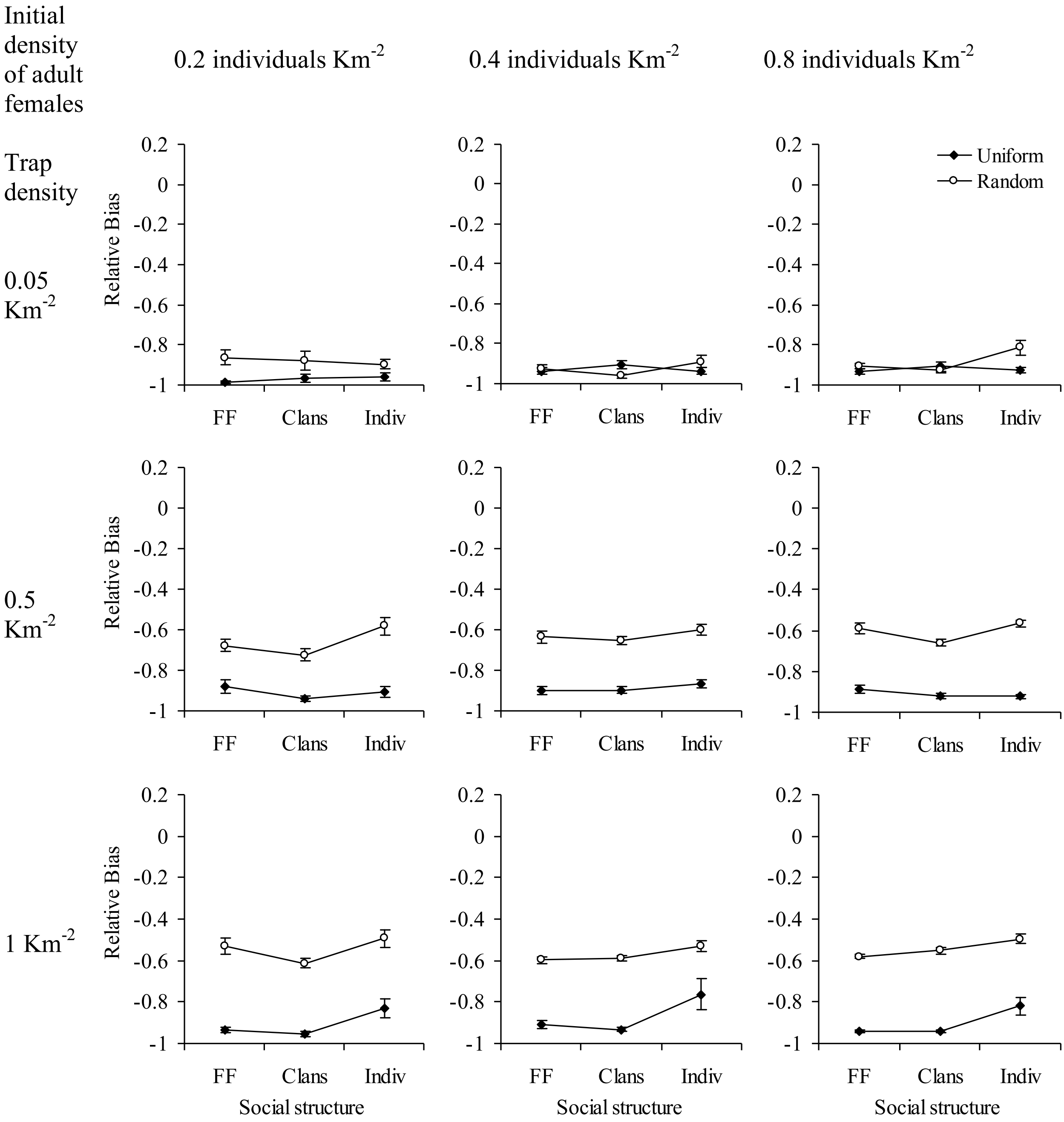

Figure 4.3. Results from Robust Design with heterogeneity for the sampling scale of four blocks: relative bias (± SE) for different social structures (FF: fission-fusion, groups within clans; Clans: only clans, Indiv: non-associating individuals) for different combinations of initial adult female density and trap density for uniform and random spatial arrangements of traps.

Table 4.1. ANOVA table for sampling scale of 16 blocks with initial female density as a factor. The dependent variable is relative bias. Factors that showed significant effects are shown in bold font.

Factor	Effect		Error		F	P value
	df	MS	df	MS		
Trap Spatial Arrangement (TSA)	1	1.763	453	0.005	330.683	<0.001
Trap Density (TD)	2	1.506	453	0.005	282.404	<0.001
Social Structure (SocS)	2	0.058	453	0.005	10.894	<0.001
Initial Female Density (IFD)	2	0.034	453	0.005	6.286	0.002
TSA x TD	2	0.519	453	0.005	97.419	<0.001
TSA x SocS	2	0.013	453	0.005	2.375	0.094
TD x SocS	4	0.106	453	0.005	19.819	<0.001
TSA x IFD	2	0.001	453	0.005	0.097	0.908
TD x IFD	4	0.002	453	0.005	0.314	0.868
SocS x IFD	4	0.009	453	0.005	1.755	0.137
TSA x TD x SocS	4	0.008	453	0.005	1.428	0.223
TSA x TD x IFD	4	0.004	453	0.005	0.679	0.607
TSA x SocS x IFD	4	0.004	453	0.005	0.751	0.558
TD x SocS x IFD	8	0.005	453	0.005	0.963	0.464
TSA x TD x SocS x IFD	8	0.004	453	0.005	0.771	0.629

Table 4.2. ANOVA table for sampling scale of nine blocks with initial female density as a factor. The dependent variable is relative bias. Factors that showed significant effects are shown in bold font.

Factor	Effect		Error		F	P value
	df	MS	df	MS		
Trap Spatial Arrangement (TSA)	1	3.144	477	0.006	530.788	<0.001
Trap Density (TD)	2	1.484	477	0.006	250.471	<0.001
Social Structure (SocS)	2	0.260	477	0.006	43.966	<0.001
Initial Female Density (IFD)	2	0.022	477	0.006	3.720	0.025
TSA x TD	2	0.648	477	0.006	109.327	<0.001
TSA x SocS	2	0.006	477	0.006	0.929	0.396
TD x SocS	4	0.043	477	0.006	7.261	<0.001
TSA x IFD	2	0.015	477	0.006	2.598	0.075
TD x IFD	4	0.001	477	0.006	0.243	0.914
SocS x IFD	4	0.003	477	0.006	0.547	0.702
TSA x TD x SocS	4	0.006	477	0.006	1.038	0.387
TSA x TD x IFD	4	0.014	477	0.006	2.333	0.055
TSA x SocS x IFD	4	0.013	477	0.006	2.273	0.060
TD x SocS x IFD	8	0.015	477	0.006	2.568	0.009
TSA x TD x SocS x IFD	8	0.005	477	0.006	0.796	0.607

Table 4.3. ANOVA table for sampling scale of four blocks with initial female density as a factor. The dependent variable is relative bias. Factors that showed significant effects are shown in bold font.

Factor	Effect		Error		F	P value
	df	MS	Df	MS		
Trap Spatial Arrangement (TSA)	1	6.321	481	0.007	926.516	<0.001
Trap Density (TD)	2	1.832	481	0.007	268.606	<0.001
Social Structure (SocS)	2	0.185	481	0.007	27.137	<0.001
Initial Female Density (IFD)	2	0.014	481	0.007	2.090	0.125
TSA x TD	2	1.042	481	0.007	152.782	<0.001
TSA x SocS	2	0.009	481	0.007	1.350	0.260
TD x SocS	4	0.039	481	0.007	5.702	<0.001
TSA x IFD	2	0.034	481	0.007	5.012	0.007
TD x IFD	4	0.006	481	0.007	0.843	0.498
SocS x IFD	4	0.003	481	0.007	0.503	0.733
TSA x TD x SocS	4	0.025	481	0.007	3.712	0.005
TSA x TD x IFD	4	0.015	481	0.007	2.191	0.069
TSA x SocS x IFD	4	0.003	481	0.007	0.509	0.729
TD x SocS x IFD	8	0.007	481	0.007	1.023	0.417
TSA x TD x SocS x IFD	8	0.008	481	0.007	1.238	0.275

Table 4.4 Fraction of Sums of Squares from the three four-way ANOVAs.

Effect	**16 Blocks, Actual Density**	**9 Blocks, Initial Density**	**4 Blocks, Actual Density**
TSA	0.436	0.553	0.662
TD	0.373	0.261	0.192
SocS	0.014	0.046	0.019
Adult Female Density (AFD)	0.008	0.004	0.001
TSA x TD	0.129	0.114	0.109
TSA x SocS	0.003	0.001	0.001
TD x SocS	0.026	0.008	0.004
TSA x AFD	0.000	0.003	0.004
TD x AFD	0.000	0.000	0.001
SocS x AFD	0.002	0.001	0.000
TSA x TD x SocS	0.002	0.001	0.003
TSA x TD x AFD	0.001	0.002	0.002
TSA x SocS x AFD	0.001	0.002	0.000
TD x SocS x AFD	0.001	0.003	0.001
TSA x TD x SocS x AFD	0.001	0.001	0.001
Error	0.001	0.001	0.001

Table 4.5 Results of pairwise Tukey's tests for the main effects in the ANOVAs for the three sets of analyses (a<b, a is not different from a,b, etc.).

	Initial Adult Female Density		
Blocks	**Trap Spatial Arrangement**	Mean	Significance
16	Uniform	-0.850	a
	Random	-0.722	b
Blocks	**Trap Spatial Arrangement**	Mean	Significance
9	Uniform	-0.870	a
	Random	-0.716	b
Blocks	**Trap Spatial Arrangement**	Mean	Significance
4	Uniform	-0.911	a
	Random	-0.694	b
Blocks	**Trap Density**	Mean	Significance
16	0.05 Km^{-2}	-0.915	a
	0.5 Km^{-2}	-0.716	b
	1.0 Km^{-2}	-0.726	b
Blocks	**Trap Density**	Mean	Significance
9	0.05 Km^{-2}	-0.900	a
	0.5 Km^{-2}	-0.747	b
	1.0 Km^{-2}	-0.732	b
Blocks	**Trap Density**	Mean	Significance
4	0.05 Km^{-2}	-0.917	a
	0.5 Km^{-2}	-0.767	b
	1.0 Km^{-2}	-0.722	c
Blocks	**Social Structure**	Mean	Significance
16	Groups within clans	-0.794	a
	Only clans	-0.801	a
	Individuals	-0.762	b
Blocks	**Social Structure**	Mean	Significance
	Groups within clans	-0.811	a
9	Only clans	-0.819	a
	Individuals	-0.749	b
Blocks	**Social Structure**	Mean	Significance
4	Groups within clans	-0.811	a
	Only clans	-0.829	a
	Individuals	-0.766	b
Blocks	**Initial Female Density**	Mean	Significance
16	0.2 Individuals Km^{-2}	-0.791	a
	0.4 Individuals Km^{-2}	-0.796	a
	0.8 Individuals Km^{-2}	-0.770	b
Blocks	**Initial Female Density**	Mean	Significance
9	0.2 Individuals Km^{-2}	-0.804	a
	0.4 Individuals Km^{-2}	-0.793	a,b
	0.8 Individuals Km^{-2}	-0.782	b
Blocks	**Initial Female Density**	Mean	Significance
4	Initial Female Density not significant		

Table 4.6 Results of pairwise comparison of the trap spatial arrangement x trap density interaction for the three analyses (a<b, a is not different from a,b, etc.).

	Initial Adult Female Density		
Blocks	**Trap Spatial Arrangement x Trap Density**	Mean	Significance
16	Uniform, 0.05 Km^{-2}	-0.911	a
	Uniform, 0.5 Km^{-2}	-0.789	b
	Uniform, 1.0 Km^{-2}	-0.848	c
	Random, 0.05 Km^{-2}	-0.919	a
	Random, 0.5 Km^{-2}	-0.642	d
	Random, 1.0 Km^{-2}	-0.603	e
Blocks	**Trap Spatial Arrangement x Trap Density**	Mean	Significance
9	Uniform, 0.05 Km^{-2}	-0.908	a
	Uniform, 0.5 Km^{-2}	-0.843	b
	Uniform, 1.0 Km^{-2}	-0.859	b,c
	Random, 0.05 Km^{-2}	-0.891	a.c
	Random, 0.5 Km^{-2}	-0.651	d
	Random, 1.0 Km^{-2}	-0.605	e
Blocks	**Trap Spatial Arrangement x Trap Density**	Mean	Significance
4	Uniform, 0.05 Km^{-2}	-0.939	a
	Uniform, 0.5 Km^{-2}	-0.903	b
	Uniform, 1.0 Km^{-2}	-0.891	b
	Random, 0.05 Km^{-2}	-0.895	b
	Random, 0.5 Km^{-2}	-0.632	c
	Random, 1.0 Km^{-2}	-0.553	d

Table 4.7 Results of pairwise comparison of trap density x social structure for the three comparisons and of trap spatial arrangement and adult female density for the 4 blocks sampling scale (a<b, a is not different from a,b, etc.).

Blocks	**Trap Density x Social Structure**	Mean	Significance
16	0.05 Km^{-2}, groups within clans	-0.886	a
	0.05 Km^{-2}, only clans	-0.905	a
	0.05 Km^{-2}, individuals	-0.954	b
	0.5 Km^{-2}, groups within clans	-0.758	c
	0.5 Km^{-2}, only clans	-0.755	c
	0.5 Km^{-2}, individuals	-0.634	d
	1 Km^{-2}, groups within clans	-0.737	c,e
	1 Km^{-2}, only clans	-0.744	c
	1 Km^{-2}, individuals	-0.696	e

Blocks	**Trap Density x Social Structure**	Mean	Significance
9	0.05 Km^{-2}, groups within clans	-0.907	a
	0.05 Km^{-2}, only clans	-0.902	a
	0.05 Km^{-2}, individuals	-0.891	a
	0.5 Km^{-2}, groups within clans	-0.765	b
	0.5 Km^{-2}, only clans	-0.787	b
	0.5 Km^{-2}, individuals	-0.689	c
	1 Km^{-2}, groups within clans	-0.760	b
	1 Km^{-2}, only clans	-0.768	b
	1 Km^{-2}, individuals	-0.667	c

Blocks	**Trap Density x Social Structure**	Mean	Significance
4	0.05 Km^{-2}, groups within clans	-0.923	a
	0.05 Km^{-2}, only clans	-0.925	a
	0.05 Km^{-2}, individuals	-0.904	a
	0.5 Km^{-2}, groups within clans	-0.762	b,c
	0.5 Km^{-2}, only clans	-0.800	b
	0.5 Km^{-2}, individuals	-0.740	c
	1 Km^{-2}, groups within clans	-0.749	c
	1 Km^{-2}, only clans	-0.763	b,c
	1 Km^{-2}, individuals	-0.655	d

Blocks	**Trap Sptial Arrangement x Adult Female Density**	Mean	Significance
4	Uniform, 0.2 Individuals Km^{-2}	-0.928	a
	Uniform, 0.4 Individuals Km^{-2}	-0.895	a
	Uniform, 0.8 Individuals Km^{-2}	-0.911	a
	Random, 0.2 Individuals Km^{-2}	-0.695	b
	Random, 0.4 Individuals Km^{-2}	-0.709	b
	Random, 0.8 Individuals Km^{-2}	-0.676	b

Table 4.8 Results of pairwise comparison of trap density x social structure x adult female density for the 9 blocks sampling scale (a<b, a is not different from a,b, etc.).

	Initial Adult Female Density		
Blocks	**Trap Density x Social Structure x Adult Female Density**	Mean	Significance
9	0.05 Km^{-2}, groups with clans, 0.2 Individuals Km^{-2}	-0.910	a
	0.05 Km^{-2}, groups with clans, 0.4 Individuals Km^{-2}	-0.908	a
	0.05 Km^{-2}, groups with clans, 0.8 Individuals Km^{-2}	-0.903	a
	0.05 Km^{-2}, only clans, 0.2 Individuals Km^{-2}	-0.897	a
	0.05 Km^{-2}, only clans, 0.4 Individuals Km^{-2}	-0.919	a
	0.05 Km^{-2}, only clans, 0.8 Individuals Km^{-2}	-0.890	a
	0.05 Km^{-2}, individuals, 0.2 Individuals Km^{-2}	-0.944	a
	0.05 Km^{-2}, individuals, 0.4 Individuals Km^{-2}	-0.870	a,b
	0.05 Km^{-2}, individuals, 0.8 Individuals Km^{-2}	-0.858	a,b,c
	0.5 Km^{-2}, groups with clans, 0.2 Individuals Km^{-2}	-0.777	c,d
	0.5 Km^{-2}, groups with clans, 0.4 Individuals Km^{-2}	-0.772	c,d,e
	0.5 Km^{-2}, groups with clans, 0.8 Individuals Km^{-2}	-0.747	d,e,g
	0.5 Km^{-2}, only clans, 0.2 Individuals Km^{-2}	-0.799	b,d
	0.5 Km^{-2}, only clans, 0.4 Individuals Km^{-2}	-0.791	b,d
	0.5 Km^{-2}, only clans, 0.8 Individuals Km^{-2}	-0.771	c,d,e
	0.5 Km^{-2}, individuals, 0.2 Individuals Km^{-2}	-0.685	e,f
	0.5 Km^{-2}, individuals, 0.4 Individuals Km^{-2}	-0.684	e,f
	0.5 Km^{-2}, individuals, 0.8 Individuals Km^{-2}	-0.698	e,f
	1 Km^{-2}, groups with clans, 0.2 Individuals Km^{-2}	-0.792	b,d
	1 Km^{-2}, groups with clans, 0.4 Individuals Km^{-2}	-0.748	d,e,g
	1 Km^{-2}, groups with clans, 0.8 Individuals Km^{-2}	-0.741	d,e,g
	1 Km^{-2}, only clans, 0.2 Individuals Km^{-2}	-0.794	b,d
	1 Km^{-2}, only clans, 0.4 Individuals Km^{-2}	-0.766	d,e,g
	1 Km^{-2}, only clans, 0.8 Individuals Km^{-2}	-0.745	d,e,g
	1 Km^{-2}, individuals, 0.2 Individuals Km^{-2}	-0.641	f
	1 Km^{-2}, individuals, 0.4 Individuals Km^{-2}	-0.678	f,g
	1 Km^{-2}, individuals, 0.8 Individuals Km^{-2}	-0.683	e,f

Table 4.9 Results of pairwise comparison of trap spatial arrangement x trap density x social structure for the 4 blocks sampling scale (a<b, a is not different from a,b, etc.).

	Initial Adult Female Density		
Blocks	**Trap Spatial Arrangement x Trap Density x Social Structure**	Mean	Significance
4	Uniform, 0.05 Km^{-2}, groups with clans	-0.950	a
	Uniform, 0.05 Km^{-2}, only clans	-0.928	a,b
	Uniform, 0.05 Km^{-2}, individuals	-0.940	a,b
	Uniform, 0.5 Km^{-2}, groups with clans	-0.890	a,b
	Uniform, 0.5 Km^{-2}, only clans	-0.920	a,b
	Uniform, 0.5 Km^{-2}, individuals	-0.899	a,b
	Uniform, 1 Km^{-2}, groups with clans	-0.929	a,b
	Uniform, 1 Km^{-2}, only clans	-0.941	a,b
	Uniform, 1 Km^{-2}, individuals	-0.804	c
	Random, 0.05 Km^{-2}, groups with clans	-0.897	a,b
	Random, 0.05 Km^{-2}, only clans	-0.922	a,b
	Random, 0.05 Km^{-2}, individuals	-0.867	b,c
	Random, 0.5 Km^{-2}, groups with clans	-0.635	d,e
	Random, 0.5 Km^{-2}, only clans	-0.679	d
	Random, 0.5 Km^{-2}, individuals	-0.582	e
	Random, 1 Km^{-2}, groups with clans	-0.569	e,f
	Random, 1 Km^{-2}, only clans	-0.585	e
	Random, 1 Km^{-2}, individuals	-0.507	f

CHAPTER 5: CONCLUSIONS

I used an individual-based simulation to examine bias in two mark-recapture population size estimation models, POPAN and Robust Design with individual heterogeneity, as applied to populations with differing social structures under differing trapping scenarios. The social structures used in the study were hierarchical groups with fission-fusion dynamics (groups within clans), fixed groups (only clans), and non-associating individuals. The fission-fusion and fixed groups cases entailed non-independence of captures between individuals which is a violation of one of the fundamental assumption of mark-recapture models, i.e., the assumption of independence of captures among individuals (Otis *et al.* 1978, Williams *et al.* 2002, Amstrup *et al.* 2005). Moreover, individuals in different groups could have different sets of capture probabilities, giving rise to individual heterogeneity in capture probability. The individual-based simulation was based on Asian elephant fission-fusion dynamics. As an initial step, the Robust Design with heterogeneity and POPAN were used because the former accounts for heterogeneity in capture probabilities although not non-independence of captures, while the latter is commonly used to estimate superpopulation sizes of open populations although it does not account for capture heterogeneity. I found that POPAN yielded estimates of superpopulation size with much lower bias than that of population size estimates from Robust Design with heterogeneity. This might have been because the population was not completely closed within each sampling block during the primary periods of Robust Design. Although the Robust Design method can still estimate superpopulation size instead of population size when there is temporary migration, it will give biased estimates if there is permanent migration (Kendall 1999). In the future, one could measure migration across blocks to check for these violations of the Robust Design assumption. An alternative strategy can be to use the open Robust Design model (Schwarz and Stobo 1997), and this model should also be tested for bias in future work. The SECR models, which model capture probabilities as a function of an individual's location with respect to the trap arrangement, should also be tested for bias using the simulated data as they presently appear to be a promising technique in estimating population size and density in case of spatially induced individual heterogeneity (Royle *et al*. 2014). There are also open population models that use mixtures of capture probabilities (Pledger *et al*. 2003, 2010) although these models have not been implemented in estimation software such as program MARK (White and Burnham 1999).

High trap densities and larger sampling scales yielded less biased estimates in general, across both models tested. Larger sampling areas reduce heterogeneity due to temporary migration, and higher trap densities should lead to capture probabilities being higher in principle. Capture probabilities >0.2 have been known to give robust estimates even in cases where there is non-independence of captures (Boulanger *et al*. 2004). Thus, capture probabilities from our analyses should be looked at in the future in order to find out what range of capture probabilities can be trusted to give unbiased estimates. I also found that the uniformly random spatial arrangement of traps performed much better than uniformly placed traps. In the current set of simulations, movement was random. Whether randomly placed traps perform equally well when directed movement is modelled would be interesting to explore. Social structure did not explain much of the variation in relative bias either in the case of POPAN or Robust Design, although it had a significant effect in most analyses with the non-associating individuals case yielding the least absolute values of relative bias in population size estimation at higher trap densities. Thus, it would be reasonable to use mark-recapture estimators in the case of species such as the Asian elephant which shows fission-fusion social dynamics, provided that overall capture probabilities are ensured to be sufficiently high. This can be achieved by using high trap densities, on the order of 0.5 to 1.0 traps Km^{-2}, and by using a non-uniform trap arrangement. It has been suggested that traps should be laid at locations where animals tend to visit often (Karanth *et al.* 2011). Consequently, a simulation modelling non-random movement should be developed in the future to test the efficacy of the different trap arrangements mention above in a more realistic situation. It would also be useful to examine how different home range sizes interact with the factors that have already been looked at. Non-independence of capture probabilities can also be modelled in the form of strictly solitary individuals, in which there is some repulsion when they approach one another and in the case of groups with dominance between groups.

Simulation studies modelling non-independence of captures in the case of grizzly bear mother-cub pairs (Boulanger *et al.* 2004), and using individual based simulations to model idiosyncratic movement in snowshoe hares (Boulanger and Krebs 1996), that tested for bias in mark-recapture estimates of population size have yielded valuable insights into sampling strategies that can be employed in those particular cases. Boulanger *et al.* (2004) showed that non-independence of captures in the case of mother-cub pairs leads to bias in population size estimates, with the closed population M_h model giving the least biased estimates, but also the largest variance. They also showed that study designs that ensure capture probabilities greater than 0.2 and population sizes greater than 50 greatly reduced bias in estimates due to non-independence of captures and individual heterogeneity in capture probabilities. Boulanger and Krebs (1996) modelled snowshoe hare movement such that capture probabilities were directly related to the nightly movement shown by an individual. They showed that the M_h closed population estimator of population gave the least biased estimates. Thus, individual based simulations provide a way to test models that estimate population size and other parameters in cases where the distribution and pattern of capture probabilities cannot be intuitively ascertained. These models often make assumptions that might not be met in real situations, but testing for violations of the assumptions is usually not possible as actual population sizes are not known for real populations. Thus, such simulations can be a powerful tool to test for bias in mark-recapture estimators in situations where clear strategies for sampling and estimation are not available.

REFERENCES

1. Ahlering, M. A., Hedges, S., Johnson, A., Tyson, M., Schuttler, S. G. & Eggert, L. S. (2011). Genetic diversity, social structure, and conservation value of the elephants of the Nakai Plateau, Lao PDR, based on non-invasive sampling. *Conservation Genetics*, 12, 413-422.
2. Alho, J. M. (1990). Logistic regression in capture-recapture models. *Biometrics*, 46, 623-635.
3. Amstrup, S. C., McDonald, T. L. & Manly, B. F. (Eds.) (2010). *Handbook of Capture-Recapture Analysis*. Princeton University Press, Princeton, New Jersey.
4. Arnason, A. N. (1972). Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Researches on Population Ecology*, 13, 97-113.
5. Arnason, A. N. (1973). The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology*, 15, 1-8.
6. Asian Elephant Research and Conservation Center (AERCC) (1998). The Asian Elephant in Southern India: A GIS Database for Conservation of Project Elephant Reserves. *Technical Report No. 6*. AERCC, Center for Ecological Sciences, IISc, Bangalore.
7. Aureli F., Schaffner C., Boesch C., Bearder S. K., Call J., Chapman C. A., Connor R., DiFiore A., Dunbar R. I. M., Henzi P. S., Holekamp K., Korstjens A. H., Layton R., Lee P., Lehmann J., Manson J. H., Ramos-Fernandez G., Strier K. B. & van Schaik C. P. (2008). Fission–fusion dynamics: new research frameworks. *Current Anthropology*, 49, 627– 654.
8. Bailey, N. T. (1952). Improvements in the interpretation of recapture data. *Journal of Animal Ecology*, 21, 120-127.

9. Baskaran, N. & Sukumar, R. (2011). Karnataka Elephant Census 2010. Technical report to the Karnataka Forest Department. Asian Nature Conservation Foundation and Indian Institute of Science, Bangalore.

10. Baskaran, N. (2002). *Ranging and Resource Utilization of Asian Elephants (Elephas maximus) in Nilgiri Biosphere Reserve*. Ph.D. Thesis, Bharathidasan University, Thiruchirapalli.

11. Baskaran, N., Balasubramanian, M., Swaminathan, S. & Desai, A. A. (1995). Home range of elephants in the Nilgiri Biosphere Reserve, south India. In (eds. Daniel, J. C. & Datye, H. S.) *A Week With Elephants: Proceedings of the International Seminar on the Conservation of Asian Elephant*. Bombay Natural History Society and Oxford University Press, Bombay, pp. 296-313.

12. Baskaran, N., Balasubramanian, M., Swaminathan, S. & Desai, A. A. (2010b). Feeding ecology of the Asian elephant *Elephas maximus* Linnaeus in the Nilgiri Biosphere Reserve, southern India. *Journal of the Bombay Natural History Society*, 107, 3-13.

13. Baskaran, N., Udhayan, A. & Desai, A. A. (2010a). Status of the Asian elephant population in Mudumalai Wildlife Sanctuary, southern India. *Gajah*, 32, 6-13.

14. Bist, S. S. (2002). An overview of elephant conservation in India. *Indian Forester*, 128, 121-136.

15. Blake, S. & Hedges, S. (2004). Sinking the flagship: the case of forest elephants in Asia and Africa. *Conservation Biology*, 18, 1191-1202.

16. Borchers, D. (2012). A non-technical overview of spatially explicit capture–recapture models. *Journal of Ornithology*, 152, 435-444.

17. Borchers, D. L. & Efford, M. G. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, 64, 377-385.

18. Boulanger, J. G. & Krebs, C. J. (1996). Robustness of capture-recapture estimators to sample biases in a cyclic snowshoe hare population. *Journal of Applied Ecology*, 33, 530-542.

19. Boulanger, J., McLellan, B. N., Woods, J. G., Proctor, M. F. & Strobeck, C. (2004). Sampling design and bias in DNA-based capture-mark-recapture population and density estimates of grizzly bears. *Journal of Wildlife Management*, 68, 457-469.

20. Bowden, D. C. & Kufeld, R. C. (1995). Generalized mark-sight population size estimation applied to Colorado moose. *Journal of Wildlife Management*, 59, 840-851.

21. Brownie, C., Hines, J. E., Nichols, J. D., Pollock, K. H. & Hestbeck, J. B. (1993). Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics*, 49, 1173-1187.

22. Bryan, T. (2004). Basic Sources of Statistics. In (eds. Swanson, D. & Siegel, J. S.) *The Methods and Materials of Demography*, 2nd ed. Elsevier Academic Press, Amsterdam, pp. 9-39.

23. Burnham, K. P. & Overton, W. S. (1978). Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika*, 65, 625-633.

24. Burnham, K. P. & Overton, W. S. (1979). Robust estimation of population size when capture probabilities vary among animals. *Ecology*, 60, 927-936.

25. Burnham, K. P., Anderson, D. R. & Laake, J. L. (1980). Estimation of density from line transect sampling of biological populations. *Wildlife Monographs*, 72, 3-202.

26. Carothers, A. D. (1973). Capture-recapture methods applied to a population with known parameters. *Journal of Animal Ecology*, 42, 125-146.

27. Carothers, A. D. (1979). Quantifying unequal catchability and its effect on survival estimates in an actual population. *Journal of Animal Ecology*, 48, 863-869.

28. Chakraborty, S., Boominathan, D., Desai, A. A. & Vidya, T. N. C. (2014). Using genetic analysis to estimate population size, sex ratio, and social organization in an Asian elephant population in conflict with humans in Alur, southern India. *Conservation Genetics*, 15, 897-907.

29. Chao, A. & Lee, S. M. (1992). Estimating the number of classes via sample coverage. *Journal of the American Statistical Association*, 87, 210-217.

30. Chao, A., Lee, S. M. & Jeng, S. L. (1992). Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics*, 48, 201-216.

31. Choudhury, A., Lahiri Choudhury, D.K., Desai, A., Duckworth, J.W., Easa, P.S., Johnsingh, A.J.T., Fernando, P., Hedges, S., Gunawardena, M., Kurt, F., Karanth, U., Lister, A., Menon, V., Riddle, H., Rübel, A. & Wikramanayake, E. (IUCN SSC Asian Elephant Specialist Group) (2008). *Elephas maximus*. In: The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 24 March 2015.

32. Clutton-Brock, T. H. & Iason, G. R. (1986). Sex ratio variation in mammals. *Quarterly Review of Biology*, 61, 339-374.

33. Clutton-Brock, T. H. (1986). Sex ratio variation in birds. *Ibis*, 128, 317-329.

34. Cochran, W. G. (1978). Laplace's ratio estimators. In (ed. David, H. A.) *Contributions to Survey Sampling and Applied Statistics*. Academic Press, New York, pp. 3-10.

35. Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika*, 51, 429-438.

36. Cubaynes, S., Pradel, R., Choquet, R., Duchamp, C., Gaillard, J.-M., Lebreton, J.-D., Marboutin, E., Miquel, C., Reboulet, A.-M., Poillot, C., Taberlet, P. & Gimenez, O.

(2010). Importance of accounting for detection heterogeneity when estimating abundance: the case of French wolves. *Conservation Biology*, 24, 621–626.

37. Darroch, J. N. (1958). The multiple-recapture census: I. Estimation of a closed population. *Biometrika*, 45, 343-359.
38. Darroch, J. N. (1959). The multiple-recapture census: II. Estimation when there is immigration or death. *Biometrika*, 46, 336-351.
39. Dawson, S. (1990) *A model to estimate density of Asian elephants (Elephas maximus) in forest habitats*. M.Sc. Thesis. University of Oxford, Oxford.
40. de Silva, S. & Wittemyer, G. (2012). A comparison of social organization in Asian elephants and African savannah elephants. *International Journal of Primatology*, 33, 1125-1141.
41. de Silva, S., Ranjeewa, A. D. & Kryazhimskiy, S. (2011a). The dynamics of social networks among female Asian elephants. *BMC Ecology*, 11, 17.
42. de Silva, S., Ranjeewa, A. D. & Weerakoon, D. (2011b). Demography of Asian elephants (*Elephas maximus*) at Uda Walawe National Park, Sri Lanka based on identified individuals. *Biological Conservation*, 144, 1742-1752.
43. Dempster, A. P., Laird, N. M. & Rubin, D. B. (1977). Maximum likelihood from incomplete data via the EM algorithm. *Journal of the Royal Statistical Society Series B (Methodological)*, 39, 1-38.
44. Desai, A. & Johnsingh, A. J. T. (1995). Social organization and reproductive strategy of the male Asian elephant (*Elephas maximus*). Abstract in (eds. Daniel J. C. & Datye H. S.) *A Week with Elephants: Proceedings of the International Seminar on the Conservation of Asian Elephant*. Bombay Natural History Society and Oxford University Press, Bombay, pp. 532.

45. Desai, A. A. & Baskaran, N. (1996). Impact of human activities on the ranging behaviour of elephants in the Nilgiri Biosphere Reserve, South India. *Journal of the Bombay Natural History Society*, 93, 559-569.

46. Douglas-Hamilton I. (1972). *On the Ecology and Behaviour of the African elephant.* Ph.D. Thesis, University of Oxford, Oxford.

47. Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, 106, 598-610.

48. Fernando, P. & Lande, R. (2000). Molecular genetic and behavioral analysis of social organization in the Asian elephant (*Elephas maximus*). *Behavioral Ecology and Sociobiology*, 48, 84-91.

49. Fernando, P., Wikramanayake, E. D., Janaka, H. K., Jayasinghe, L. K. A., Gunawardena, M., Kotagama, S. W., Weerakoon, D. & Pastorini, J. (2008). Ranging behavior of the Asian elephant in Sri Lanka. *Mammalian Biology*, 73, 2-13.

50. Frankham, R. (1995). Effective population size/adult population size ratios in wildlife: a review. *Genetical Research*, 66, 95-107.

51. Gardner, B., Reppucci, J., Lucherini, M. & Royle, J. A. (2010). Spatially explicit inference for open populations: estimating demographic parameters from camera-trap studies. *Ecology*, 91, 3376-3383.

52. Gaucherel, C., Balasubramanian, M., Karunakaran, P. V., Ramesh, B. R., Muthusankar, G., Hély, C. & Couteron, P. (2010). At which scales does landscape structure influence the spatial distribution of elephants in the Western Ghats (India)? *Journal of Zoology*, 280, 185-194.

53. Gilbert, R. O. (1973). Approximations of the bias in the Jolly-Seber capture-recapture model. *Biometrics*, 29, 501-526.

54. Ginsberg, J. R., & Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, 44, 377-379.

55. Goswami, V. R., Madhusudan, M. D. & Karanth, K. U. (2007). Application of photographic capture–recapture modelling to estimate demographic parameters for male Asian elephants. *Animal Conservation*, 10, 391-399.

56. Graunt, J. (1939). *Natural and Political Observations made upon the Bills of Mortality*. (Ed. Willcox, W. F.), The Johns Hopkins Press, Baltimore.

57. Gray, T. N., Vidya, T. N. C., Potdar, S., Bharti, D. K. & Sovanna, P. (2014). Population size estimation of an Asian elephant population in eastern Cambodia through non-invasive mark-recapture sampling. *Conservation Genetics*, 15, 803-810.

58. Hald, A. (2003). *A History of Probability and Statistics and their Applications before 1750*. John Wiley & Sons, New Jersey.

59. Hedges, S. & Lawson, D. (2006). Dung survey standards for the MIKE programme. *CITES MIKE Programme, Nairobi, Kenya*. *Website: www.cites.org/eng/prog/MIKE/index.shtml*.

60. Hedges, S., Johnson, A., Ahlering, M., Tyson, M. & Eggert, L. S. (2013). Accuracy, precision, and cost-effectiveness of conventional dung density and fecal DNA based survey methods to estimate Asian elephant (*Elephas maximus*) population size and structure. *Biological Conservation*, 159, 101-108.

61. Hestbeck, J. B., Nichols, J. D. & Malecki, R. A. (1991). Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology*, 72, 523-533.

62. Huggins, R. M. (1989). On the statistical analysis of capture experiments. *Biometrika*, 76, 133-140.

63. Huggins, R. M. (1991). Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics*, 47, 725-732.

64. Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, 52, 225-247.

65. Jones, J. P., Asner, G. P., Butchart, S. H. & Karanth, K. U. (2013). The ‘why’,‘what’ and ‘how’of monitoring for conservation. *Key Topics in Conservation Biology*, 2, 327-343.

66. Karanth, K. U. & Sunquist, M. E. (1992). Population structure, density and biomass of large -herbivores in the tropical forests of Nagarahole, India. *Journal of Tropical Ecology*, 8, 21-35.

67. Karanth, K. U., Nichols, J. D. & Samba Kumar, N. (2011). Estimating tiger abundance from camera trap data: field surveys and analytical issues. In (eds. O'Connell, A. F., Nichols, J. D. & Karanth, K. U.) *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, Tokyo, pp. 97-117.

68. Kemf, E. & Santiapillai, C. (2000). *Asian Elephants in the Wild*. WWF International's Species Conservation Unit, WWF, Gland, Switzerland.

69. Kendall, W. L. & Bjorkland, R. (2001). Using open robust design models to estimate temporary emigration from capture—recapture data. *Biometrics*, 57, 1113-1122.

70. Kendall, W. L. & Pollock, K. H. (1992). The robust design in capture-recapture studies: a review and evaluation by Monte Carlo simulation. In (eds. McCullough, D. R. & Barrett R. H.) *Wildlife 2001: Populations*. Elsevier Applied Science, New York, pp. 31-43.

71. Kendall, W. L. (1999). Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology*, 80, 2517-2525.

72. Kendall, W. L., Nichols, J. D. & Hines, J. E. (1997). Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology*, 78, 563-578.

73. Kendall, W. L., Pollock, K. H. & Brownie, C. (1995). A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics*, 51, 293-308.

74. Kingsland, S. E. (1995). *Modeling Nature: Episodes in the History of Population Ecology*, 2nd edition. University of Chicago Press, Chicago.

75. Kumar, M. A., Mudappa, D. & Raman, T. S. (2010). Asian elephant *Elephas maximus* habitat use and ranging in fragmented rainforest and plantations in the Anamalai Hills, India. *Tropical Conservation Science*, 3, 143-58.

76. Kummer, H. (1971). *Primate Societies: Group Techniques of Ecological Adaptation*. Aldine-Atherton, Chicago.

77. Kurt, F. (1974). Remarks on the social structure and ecology of the Ceylon elephant in the Yala National Park. In (eds. Geist, V. & Walther, F.) *The Behaviour of Ungulates and its Relation to Management*. International Union for Conservation of Nature and Natural Rsources, Morges, Switzerland, pp.618-634.

78. Laake, J.L. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

79. Le Cren, E. D. (1965). A note on the history of mark-recapture population estimates. *Journal of Animal Ecology*, 34, 453-454.

80. Lebreton, J. D., Burnham, K. P., Clobert, J. & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, 62, 67-118.

81. Lee, S. M. & Chao, A. (1994). Estimating population size via sample coverage for closed capture-recapture models. *Biometrics*, 50, 88-97.

82. Lincoln, F.C. (1930) Calculating waterfowl abundance on the basis of banding returns. *U.S. Department of Agriculture, Circular* 118, 1–4.

83. MacQueen, J. (1967). Some methods for classification and analysis of multivariate observations. In (eds. Le Cam, L. M. & Neyman, J.) *Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability*. University of California Press, Berkeley, pp. 281-297.

84. MathWorks® Inc. (2011). MATLAB Release 2011a. The MathWorks, Inc., Natick.

85. McKay, G. M. (1973). Behavior and ecology of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology*, 125, 1-113.

86. Missiakoulis, S. (2010). Cecrops, King of Athens: the first (?) recorded population census in history. *International Statistical Review*, 78, 413-418.

87. Moss C. J. & Poole J. H. (1983). Relationships and social structure of African elephants. In (ed. Hinde, R.) *Primate Social Relationships*. Blackwell, Boston, pp. 315-325.

88. Nichols, J. D. & Kendall, W. L. (1995). The use of multi-state capture-recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics*, 22, 835-846.

89. Nichols, J. D., Hines, J. E., Pollock, K. H., Hinz, R. L. & Link, W. A. (1994). Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. *Ecology*, 75, 2052-2065.

90. Norris III, J. L. & Pollock, K. H. (1996). Nonparametric MLE under two closed capture-recapture models with heterogeneity. *Biometrics*, 52, 639-649.

91. Nunney, L. & Elam, D. R. (1994). Estimating the effective population size of conserved populations. *Conservation Biology*, 8, 175-184.

92. Otis, D. L., Burnham, K. P., White, K. P. & Anderson, D. R. (1978). Statistical inference for capture data from closed populations. *Wildlife Monographs*, 62, 135 pp.

93. Payne, K. B., Langbauer Jr, W. R. & Thomas, E. M. (1986). Infrasonic calls of the Asian elephant (*Elephas maximus*). *Behavioral Ecology and Sociobiology*, 18, 297-301.

94. Petersen, C. G. J. (1889). Fiskeriberetning, 1888-1889.

95. Petersen, C. G. J. (1894). On the biology of our flat-fishes and on the decrease of our flat-fish fisheries. *Report of the Danish Biological Station*, IV.

96. Pledger, S. (2000). Unified maximum likelihood estimates for closed capture–recapture models using mixtures. *Biometrics*, 56, 434-442.

97. Pledger, S., Pollock, K. H. & Norris, J. L. (2003). Open Capture-Recapture Models with Heterogeneity: I. Cormack-Jolly-Seber Model. *Biometrics*, 59, 786-794.

98. Pledger, S., Pollock, K. H. & Norris, J. L. (2010). Open capture–recapture models with heterogeneity: II. Jolly–Seber model. *Biometrics*, 66, 883-890.

99. Pollock, K. H. (1981). Capture-recapture models allowing for age-dependent survival and capture rates. *Biometrics*, 37, 521-529.

100. Pollock, K. H. (1982). A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management*, 46, 752-757.

101. Pollock, K. H., Hines, J. E. & Nichols, J. D. (1984). The use of auxiliary variables in capture-recapture and removal experiments. *Biometrics*, 40, 329-340.

102. Pollock, K. H., Nichols, J. D., Brownie, C. & Hines, J. E. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs*, 107, 3-97.

103. Pradel, R. (2005). Multievent: an extension of multistate capture–recapture models to uncertain states. *Biometrics*, 61, 442-447.

104. R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/.

105. Rousseeuw, P. J. (1987). Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics*, 20, 53-65.

106. Royle, J. A. and Gardner, B. (2010). Hierarchial spatial capture–recapture models for estimating density from trapping arrays. In (eds. O'Connel, A. F., Nichols, J. D. & Karanth, K. U.) *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, New York, pp. 163–190.

107. Royle, J. A., Chandler, R. B., Sollmann, R. & Gardner, B. (2014). *Spatial Capture-Recapture*. Academic Press, Waltham.

108. Royle, J. A., Karanth, K. U., Gopalaswamy, A. M. & Kumar, N. S. (2009a). Bayesian inference in camera trapping studies for a class of spatial capture-recapture models. *Ecology*, 90, 3233-3244.

109. Royle, J. A., Nichols, J. D., Karanth, K. U. & Gopalaswamy, A. M. (2009b). A hierarchical model for estimating density in camera-trap studies. *Journal of Applied Ecology*, 46, 118-127.

110. Schnabel, Z. E. (1938). The estimation of total fish population of a lake. *American Mathematical Monthly*, 45, 348-352.

111. Schwarz, C. J. & Arnason, A. N. (1996). A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics*, 52, 860-873.

112. Schwarz, C. J. & Stobo, W. T. (1997). Estimating temporary migration using the robust design. *Biometrics*, 53, 178-194.

113. Schwarz, C. J., Schweigert, J. F. & Arnason, A. N. (1993). Estimating migration rates using tag-recovery data. *Biometrics*, 49, 177-193.

114. Seber, G. A. F (1984). *Multivariate Observations*. John Wiley & Sons, New Jersey.

115. Seber, G. A. F. (1965). A note on the multiple-recapture census. *Biometrika*, 52, 249-259.

116. Seber, G. A. F. (1982). *The Estimation of Animal Abundance and Related Parameters*. MacMillan Press, New York.

117. Spendelow, J. A., Nichols, J. D., Nisbet, I. C., Hays, H. & Cormons, G. D. (1995). Estimating annual survival and movement rates of adults within a metapopulation of Roseate Terns. *Ecology*, 76, 2415-2428.

118. Srinivasaiah, N. M., Anand, V. D., Vaidyanathan, S. & Sinha, A. (2012). Usual populations, unusual individuals: insights into the behavior and management of Asian elephants in fragmented landscapes. *PloS One*, 7, e42571.

119. Stageritis A. (1815). *Ogygia or Archaeology*. In Greek, J. Tsveque, Vienna (as cited in Missiakoulis 2010).

120. StatSoft, Inc. (1996). STATISTICA for Windows [Computer program manual]. Tulsa. http://www.statsoftinc.com.

121. Stigler, S. M. (1986). *The History of Statistics: The Measurement of Uncertainty Before 1900*. The Belknap Press of Harvard University Press, Cambridge.

122. Sukumar, R. & Santiapillai, C. (1996). *Elephas maximus*: status and distribution. In (eds. Shoshani, J. & Tassy, P.) *The Proboscidea: Evolution and Palaeoecology of Elephants and their Relatives*, Oxford University Press, Oxford, pp. 327-331.

123. Sukumar, R. (1989a). *The Asian Elephant: Ecology and Management*. Cambridge University Press, Cambridge.

124. Sukumar, R. (1989b). Ecology of the Asian elephant in southern India. I. Movement and habitat utilization patterns. *Journal of Tropical Ecology*, 5, 1-18.

125. Sukumar, R. (1990). Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. *Journal of Tropical Ecology*, 6, 33-53.

126. Sukumar, R. (2003). *The Living Elephants: Evolutionary Ecology, Behaviour, and Conservation*. Oxford University Press, New York.

127. Sukumar, R., Ramakrishnan, U. & Santosh, J. A. (1998). Impact of poaching on an Asian elephant population in Periyar, southern India: a model of demography and tusk harvest. *Animal Conservation*, 1, 281-291.

128. Swanson, D.A. & Stephan, G.E. (2004). A Demography Time Line. In (eds. Swanson, D. & Siegel, J.S.) *The Methods and Materials of Demography*, 2nd ed. Elsevier Academic Press, Amsterdam, pp. 9–42.

129. Turchin, P. (2003). *Complex Population Dynamics: a Theoretical/Empirical Synthesis*. Princeton University Press, Princeton.

130. Varman, K. S., Ramakrishnan, U. & Sukumar, R. (1995). Direct and indirect methods of counting elephants: a comparison of results from Mudumalai Sanctuary. In (eds. Daniel, J. C. & Datye, H. S.) *A Week With Elephants: Proceedings of the International Seminar on the Conservation of Asian Elephant*. Bombay Natural History Society and Oxford University Press, Bombay, pp. 331-339.
131. Vidya, T. N. C. & Sukumar, R. (2005). Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from microsatellite DNA. *Journal of Ethology*, 23, 205-210.
132. Vidya, T. N. C., Fernando, P., Melnick, D. J., & Sukumar, R. (2005). Population differentiation within and among Asian elephant (*Elephas maximus*) populations in southern India. *Heredity*, 94, 71-80.
133. Vidya, T. N. C., Varma, S., Dang, N. X., Van Thanh, T. & Sukumar, R. (2007). Minimum population size, genetic diversity, and social structure of the Asian elephant in Cat Tien National Park and its adjoining areas, Vietnam, based on molecular genetic analyses. *Conservation Genetics*, 8, 1471-1478.
134. White, G. C. & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46, S120-S139.
135. Williams, A. C., Johnsingh, A. J. T. & Krausman, P. R. (2007). Population estimation and demography of the Rajaji National Park elephants, North-West India. *Journal of the Bombay Natural History Society*, 104, 145-152.
136. Williams, A. C., Johnsingh, A. J. T., Krausman, P. R. & Qureshi, Q. (2008). Ranging and habitat selection by Asian elephants (*Elephas maximus*) in Rajaji National Park, North West India. *Journal of the Bombay Natural History Society*, 105, 145-155.
137. Williams, B. K., Nichols, J. D. & Conroy, M. J. (2002). *Analysis and Management of Animal Populations*. Academic Press, San Diego.

138. Wittemyer, G., Douglas-Hamilton, I. & Getz, W. M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour*, 69, 1357-1371.