Chapter 4

Estimating abundance for a savanna elephant population using mark-resight methods: a case study for the Tembe Elephant Park, South Africa

Introduction[9]

Savanna elephants and fire affect vegetation (Dublin, Sinclair & McGlade 1990; Lock 1993; Cumming *et al*. 1997; Trollope *et al*. 1998; van de Vijver, Foley & Olff 1999). Elephants confined to the Tembe Elephant Park (hereafter TEP) in South Africa are well protected, and their apparent increase may have negative consequences for sensitive vegetation types such as sand forests that support high levels of endemicity (van Wyk 1994; Matthews *et al*. 2001). The future management of this population may involve its inclusion in a transfrontier conservation area (World Bank 1996). Through this action traditional migratory patterns may be reinstated thereby reducing local pressure on sensitive ecotypes within the Park. Knowing the number of elephants present within the Park therefore has considerable conservation implications.

The techniques used to estimate population size or densities for medium to large mammals living in wooded areas are poorly developed (Caro 1999). For African elephants (*Loxodonta africana*), census methods such as dung counts (Walsh & White 1999; Walsh *et al*. 2001), aerial surveys (Whitehouse, Hall-Martin & Knight 2001; Jachmann 2002; Khaemba & Stein 2002), and calling patterns (Payne, Thompson &

[9] Chapter 4 has been drafted as an independent publication and much of the information provided here therefore repeats that in Chapter 1.

Kramer 2003) are often inadequate for small populations in dense habitats. Although aerial survey methods are well developed for open habitats (for review see Craig 1993), indirect methods are used for elephants occurring in dense habitats (for review see Barnes 1993). Whitehouse *et al*. (2001) showed that for small populations (~250) aerial surveys underestimate numbers. This problem increases with increasing population size (Whitehouse *et al*. 2001). Under such conditions, where the use of other methods is unviable, the use of mark-recapture methods could be evaluated (Walsh & White 1999). To the best of my knowledge such a method has not been applied to elephants.

Earlier attempts to count elephants in the TEP were based on aerial surveys similar to those traditionally used across much of Africa (*i.e.* Buechner *et al*. 1963; Laws 1969a; Eltringham 1977; Ottichilo 1986, 1999; St Gibson, Craig & Masogo 1998; Whitehouse *et al*. 2001; Jachmann 2002). A total count based on helicopter survey at the onset of my study yielded 65 elephants for the Park (Matthews 2000). However, a mid-day count at water holes from the same helicopter the following day yielded 74 elephants. Neither of these counts provided confidence limits. My study was designed, therefore, to evaluate the validity of a variety of mark-recapture models (see Krebs 1999) to estimate population size when applied to a confined population of elephants. The advantage of my approach is that mark-recapture procedures provide an opportunity to determine accuracy and precision for estimates derived from mark-recapture models and compare these to a registration count (where the number of known individuals are counted and registered during repeated survey), given the assumption that registration count and the mark-recapture estimates are independent. These estimates may have implications for the design of programmes to determine population size.

Materials and Methods

Study Site

The TEP covers an area of about 300 km^2 in northern KwaZulu-Natal, South Africa. Mean annual precipitation for the region is 800-1 000 mm (Schulze 1997) but is highly variable. Mean annual temperature is 20-22^{o}C. The Park's northern boundary forms the international border with Mozambique and it is surrounded by an elephant-proof fence. Situated in the Maputaland Centre of Endemism (van Wyk 1994), TEP is considered vital for the protection of regional biodiversity. There are few other protected areas in the region conserving stands of endemic-rich sand forests (van Wyk & Smith 2001). The confinement of elephants to the TEP since 1989 is artificial and may have negative consequences for sensitive vegetation communities within the Park.

Methods

I was an observer on an attempted total count using a helicopter during the last week of August, 2000. Twenty five parallel north/south orientated transects, 1km apart, of between 3km and 23km long, totalling approximately 380km, were flown at ~40 knots, at an altitude of 90m above ground level. The count was completed in two sessions, one early morning and one late afternoon. Permanent water bodies in the Muzi swamp and artificially supplemented water holes (n=4) were flown the following day between 12h00 and 14h00, the hottest part of the day.

I used a modification of Caughley's 'sequence of decisions by which a technique for estimating abundance can be chosen' (Krebs 1999) to select mark-recapture methods to determine population size. As elephants during the study were "marked" through the recording of their unique markings and thereafter resighted, all methods are hereafter referred to as mark-resight methods (see Minta & Mangel 1989).

An advantage of this mark-resight method is that animals do not have to be physically captured and handled. It allows for the post-hoc manipulation of data for both the continuous marking of the population, and non-continuous marking, as required by Bowden's estimator (Krebs 1999). Mark-resight techniques allow for the use of many mark-resight models and for accuracy and precision to be estimated (Pollock 2000).

My mark-resight protocol was based on individual identification using features such as ear markings and tears, tail characteristics, tusk form, wear and breakages, trunk and other scars (see Douglas-Hamilton 1972; Croze 1974; Jachmann 1980; Whitehouse & Hall-Martin 2000; Moss 2001). Each identifiable feature was considered a 'mark' on that individual, and all individuals carried multiple marks. These marks are considered permanent although additional marks may have been added during the study. Identification was aided by profiles including photographs and field drawings kept on references files. Elephants could be positively identified as 'marked' or 'unmarked' at time of observation. Where models allowed, unmarked animals, once encountered and marked, were added to the 'marked' population.

For elephant bulls an initial marking programme, where bulls were identified throughout the Park, was conducted over four months, during which 52 individuals were 'marked' and their identification profiles compiled. This period of familiarization facilitated accurate individual identification. The 'marking' event was then followed by 14 resighting events, each lasting 10 days each, at intervals of seven days over a period of nine months, therefore the attempt at total registration took 13 months. During each of these events the entire Park was covered by vehicle using a road network, divided into 20 sections covered by five routes. Sessions were conducted morning and afternoon, avoiding the heat of mid-day when elephants are known to be less active (Wyatt & Eltringham 1974). Resighting sessions included observations at the two main permanent water points in the Muzi swamp and the semi-permanent pan in the south of the Park. Elephants encountered during these resighting sessions, either along the routes or at waterholes, were noted as 'marked' or 'unmarked'.

I compiled group identification keys for family groups using a similar method to that used for bulls. During an initial marking period of two months, eight adult cows from different groups were 'marked' including three fitted with satellite/radio collars as part of another study. Once herds could be recognised by the identification of a 'marked' adult cow the remaining members were identified as described using the protocol of Moss (2001). Identifying features of herd animals were repeatedly noted to improve estimates of herd size. The population estimate for breeding herds is based on the repetitive enumeration of individual groups and Bowden's estimator (Krebs 1999) calculated from the sighting frequencies of the eight marked cows.

My registration count, directed at determining the total number of elephants in the population, is not reliant on a set of assumptions (Caughley & Sinclair 1994). As the sum of all the animals identified during the study it gives an estimate of the animals known to be present in the research area but is not considered a total count as new animals were recorded until the last cycle.

Data analyses

Closed Population Estimators

Mark-resight models for closed populations provide estimators that are robust to variation in capture probabilities, especially when the assumption of a closed population is valid (Kendall 1999). The assumption of a closed population is valid for this fenced population.

I used Seber's modification of the Petersen method (Seber 1982) for a single marking and a single recapture event to reduce potential bias in overestimating population size (Krebs 1999). I also assessed the data using the Schnabel method (an extension of the Petersen method) that makes the same assumptions as the Petersen method, but it is easier to identify violations of these assumptions. Here marking occurs at each of the sampling times, and only two types of individuals need be identified, marked and seen once or more before, and unmarked and not seen before (Krebs 1999).

The Schumacher-Eschmeyer estimator (referred to as the Schumacher method) is a robust and useful ecological model for multiple censuses of closed populations (Seber 1982) and allows for the non-random capture of marked and unmarked individuals (Koper & Brooks 1998). The population estimate is obtained from the slope of the linear regression of the assumed significant relationship between the proportion of animals marked (y) and those previously marked (x) (Koper & Brooks 1998). For my study this relationship was significant (y = 0.113x+0.214, r^2= 0.69, $F_{1,12}$=6.70, P<0.001).

Open Population Estimators

I used the Jolly-Seber model that also allows for the estimation of parameters such as survival. This type of open population estimator is, however, of more use for long-term programmes where populations cannot be assumed as closed (Pollock *et al*. 1990).

Model Assumptions

Generally as models become more complex they make more assumptions. For some models compliance with these assumptions can be tested for (see Table 4.1). As the equal catchability assumption is the Achilles' heel of all estimates that uses marked animals (Krebs 1999), a combination of open (Jolly-Seber) and closed (Schnabel) methods has been developed (Pollock 1982).

The Robust Capture-Recapture design allows for relatively unbiased estimates when the underlying assumptions of models are not met (Pollock 1982; Pollock *et al*. 1990; Nichols 1992), and avoids relying solely on sensitive Jolly-Seber models (Pollock *et al*. 1990; Krebs 1999).

Frequency of capture analysis operates on the number of animals caught once, twice three times and so on over several capturing sessions (see Caughley 1977). These data form a zero-truncated frequency distribution of captures, the missing zero-class representing the unknown number of animals that were never caught. The analysis estimates the frequency of zero-classes from the shape of the truncated distribution. While the Poisson estimate is reliant on constant catchability, the negative binomial estimate allows for unequal sighting (Caughley 1977).

Table 4.1. Assumptions of the mark-recapture (resight) models used to estimate population size for the Tembe Elephant Park (see Caughley 1977, Krebs 1999). Bowden's Estimator is the model with the fewest constraints when a population is closed.

	Model							
Assumption	Petersen	Schnabel	Schumacher	Jolly-Seber	JS Robust	Bowden	Poisson	Negative Binomial
Population is closed	Yes	Yes	Yes	No	No	Yes	No	No
All animals have same probability of sighting in first sample	Yes	Yes	Yes	Yes	Yes	Yes	No	No
Marking does not affect catchability	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Marks are not lost	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Sighting probabilities are equal	Yes	Yes	Yes	Yes	No	No	Yes	No
All marks are recorded in subsequent samples	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes

Bowden's estimator is a frequency of capture model, and is an extension of Petersen type population estimators developed from the Minta-Mangel model (Minta & Mangel 1989) and is available on the program NOREMARK (White 1996a) and MARK-RECAPTURE (Krebs 1999). It is a frequency of capture model that can be used for populations where individuals can be identified as marked. It is designed for closed populations and relaxes the assumption that all individuals have the same resighting probability (Krebs 1999). White (1996b) recommends the use of Bowden's estimator when there is heterogeneity of sighting probabilities. Additionally, it does not require that the entire study area be searched during the sighting period and applies even when some animals are always seen in large groups and frequently observed, while lone animals are rarely sighted (Bowden & Kufeld 1995). If mortality or emigration is independent of an animal's marked status this model remains valid.

The assumption that the population is closed was valid as TEP is fully fenced. There was effectively no recruitment to be considered as newly born calves are easily recognised and not included in the database used for estimating population size. Five adult males died during the two years of the study (see Chapter 5), some of which might have been marked, and this could have reduced the number of marked animals. Bowden's estimator, however, allows for losses providing they are independent of the mark status of the animal (Bowden & Kufeld 1995). The assumption of equal catchability is usually violated in field studies (Pollock *et al*. 1990) and can be tested for in some models. To attempt to comply with this assumption, animals were sighted and marked throughout the Park using all available roads and hides, thereby covering all areas utilised by elephants. Resighting locations and a satellite tracking study indicated that elephants move extensively throughout TEP and therefore could be encountered on any road or at any hide. Compliance with the assumption that marking does not affect catchability was ensured because a non-invasive marking method was used. A zero-truncated Poisson test (Krebs 1999) showed unequal sighting probability, as is usual under field conditions (Eberhardt 1969; Seber 1986; Pollock *et al*. 1990). The Bowden's estimator and Pollock's robust design relax the assumption of equal catchability so avoid this assumption. The Robust design allows relatively unbiased estimates to be obtained when the assumption of equal catchability is not met (Pollock 1982; Nichols 1992).

The use of naturally occurring, permanent features unique to the elephants that are known to persist over the long term (Douglas-Hamilton 1972; Croze 1974;

Jachmann 1980; Moss 2001) ensured that marks were not lost. The assumption that all marks are recorded at each subsequent observation was not violated as elephants had sufficient marks to ensure that they could be identified.

Analysis

I analysed the resight data under eight different mark-resight models using the software MARK-RECAPTURE (in Programs for Ecological Methodology 2nd Edition Krebs 1999). I used least squares linear regression analysis (Sokal & Rohlf 1995) to illustrate trends in the accuracy and precision of the models when effort increases. I used the small sample unbiased Akaike information criterion (AIC_c) to evaluate fit and complexity for the resight models used (see Johnson & Omland 2004 and references therein).

Results

Population Size

The helicopter count yielded a population estimate of 65 elephants. Of these 25 were bulls and 19 were cows. Twenty one elephants were classified as sub-adults or younger elephants for which sex could not be assigned from the air. The 65 elephants occurred in 20 groups (sightings). The mid-day water hole count yielded 74 elephants, 29 bulls, 14 cows and 31 sub-adults or younger.

From the registration count I identified 75 bulls, 52 of these before the resighting sessions. During the 14 sighting sessions I encountered 42 of the 52 pre-identified bulls and an additional 23 bulls. Of the 52 pre-identified bulls 10% were observed in the last four cycles (two months) of the study. For the 23 additional bulls, 17% were recorded in the last four cycles. From observations of the eight marked cows in breeding herds and the recognition of known adult cows and their attendant young, before, during and after resighting sessions, I identified 92 elephants in ten family units. When I combined observations of breeding herds and bulls I obtained a 'known-to-be-alive' count of 167 elephants for TEP.

The resighting sessions yielded 65 different bulls on 189 occasions. After 14 sessions, all population estimates for bulls, except for the negative binomial (n=87, 95% CI=65-126), were lower than that obtained using the registration count (Poisson (n=70, 95% CI=55-86), Bowden's estimator (n=67, 95% CI=60-74), Jolly-Seber (n=63, 95% CI=3-123), Schumacher (n=61, 95% CI=54-69), Schnabel (n=59, 95% CI=49-73), Robust (n=55, 95% CI=45-79), Petersen (n=38, 95% CI=27-79)) (Fig. 4.1a). Only the Poisson and Bowden's models yielded estimates close to the registration count.

The only sight-resight model suitable for estimating the population size of the breeding herds was Bowden's estimator. Other models require all animals to be identified as marked or unmarked upon capture (sighting). This could not be determined for all animals at every breeding herd observation. The Bowden's estimator allowed population estimates when some marked animals are not identified at every sighting (Bowden & Kufeld 1995).

The 14 sighting events yielded marked cows on 16 occasions and all of the marked cows were sighted at least once. When all sightings of breeding herds post-marking are included, breeding herds were sighted on 37 occasions and all marked cows were sighted at least three times each. The estimates for breeding herds, both for sighting events and when all sightings are considered exceed the 'known to be alive' estimate (Fig. 4.1b).

The Bowden's estimator (all breeding herd sightings) yielded an estimate of 179 elephants for the Park (Fig. 4.2), 4% higher than the number of animals known to be alive for the population. For sighting sessions, the Bowden's estimator under-estimated the registration count for bulls by 11%, and over-estimated the breeding herd registration by 15%.

For the total population Bowden's estimator exceeded the waterhole count by 60% and the registration count by 6.7%. The helicopter survey under-counted the Bowden's estimator by 65% and the registration count by 61% (Fig. 4.2).

Influence of effort on estimates

I used least squares linear regression analysis to determine the influence of effort on the estimates and here consider accuracy in terms of the match of an estimate generated by a given model to the population size, as deduced from the registration record compiled for the population.

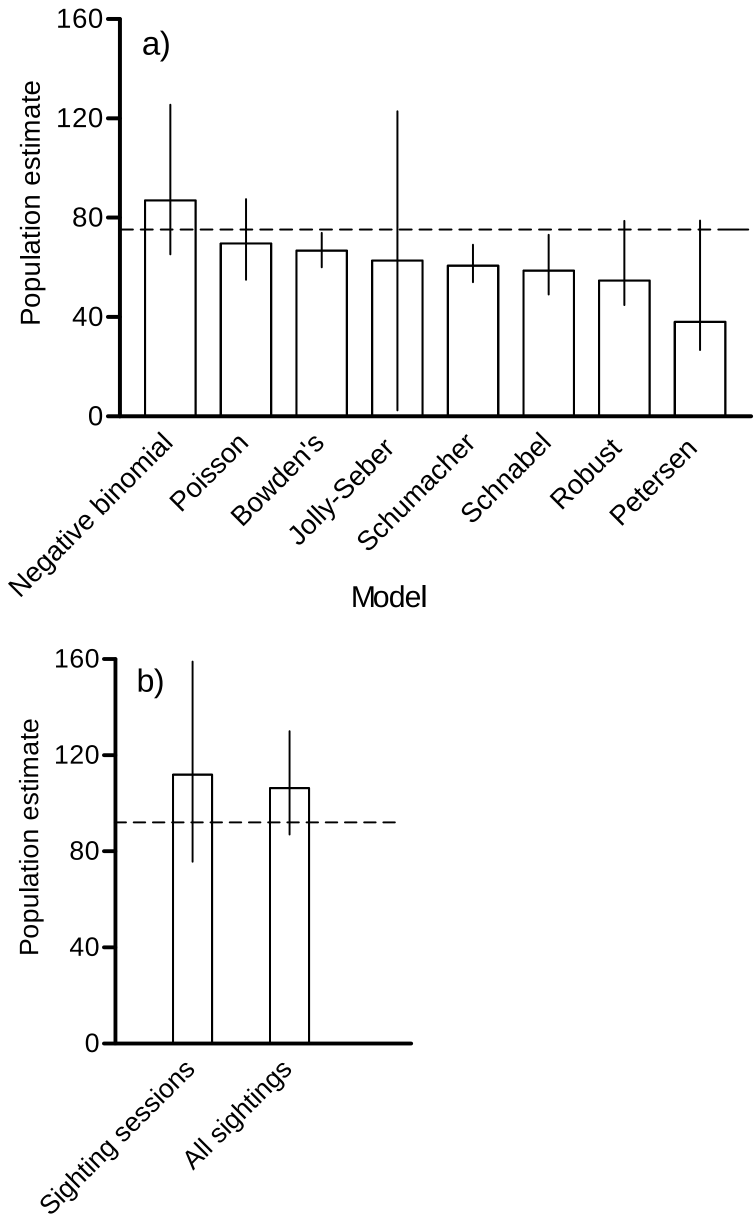


Figure 4.1. Population estimates for sight-resight models for (a) elephant bulls and (b) elephant breeding herds in the Tembe Elephant Park. For breeding herds only Bowden's estimator was used. Estimates for bulls are based on 14 sighting sessions. For breeding herds population size was determined from 14 sighting sessions, indicated as 'sighting sessions' and from all post marking observations, indicated as 'all sightings'. Bars indicate population estimate, vertical lines indicate 95% confidence intervals. Dashed line denotes the number determined by registration counts.

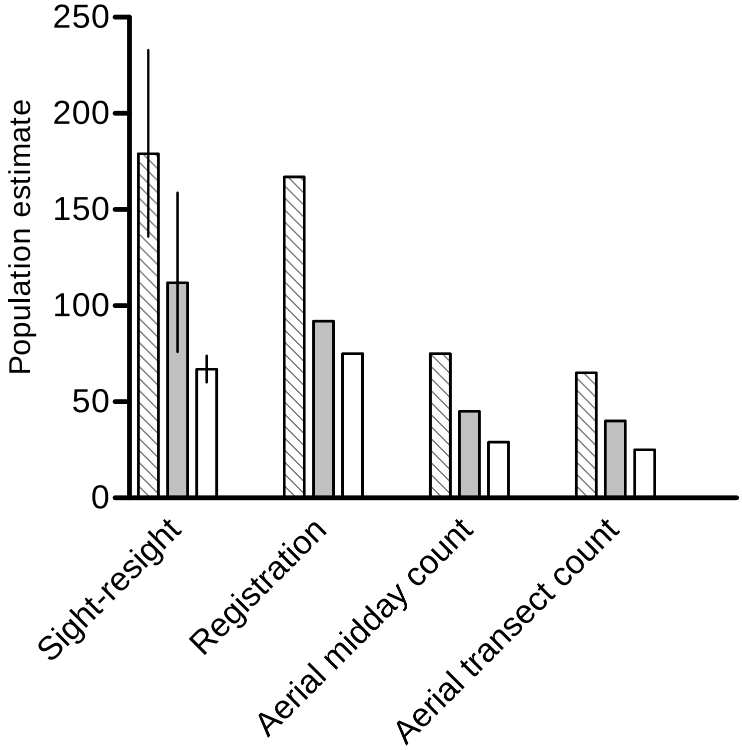


Figure 4.2. Comparison of population estimates determined from the Bowden's estimator (sight-resight method), registration count and two aerial counting methods. Total population estimates are indicated by bars with lined fillings, animals in breeding herds by shaded bars and bulls by open bars. Vertical lines indicate 95% confidence intervals.

For bulls the estimate generated by the negative binomial model was not affected by effort (y=57.39+2.637x, r^2=0.32, $F_{1,10}$ = 4.60, P=0.058) but for all other models estimates improved with increasing effort (Poisson, y=50.61+1.220x, r^2= 0.70, $F_{1,10}$= 23.20, P<0.001, Bowden's, y=60.65+0.577x, r^2=0.70, $F_{1,12}$ =28.36, P<0.001, Jolly-Seber, y=10.41+3.392x, r^2=0.51, $F_{1,10}$ = 10.44, P<0.05, Schumacher, y=37.71+1.737x, r =0.86, $F_{1,10}$=63.64, P<0.0001, Schnabel, y=37.45+1.619x, r^2=0.90, $F_{1,10}$=91.73, P<0.0001; Fig. 4.3 a-f).

Limiting the analysis to data collected during structured resighting sessions, estimates did not improve with increasing effort (y=83.18+2.901x, $F_{1,5}$=4.63, P=0.084; Fig. 4.4a). When all observations of breeding herds are included in the analysis, however, estimates of population size improve with increasing effort (y=76.33+1.013x, $F_{1,35}$=49.28, P<0.0001; Fig. 4.4b).

The influence of effort on precision

Effort only affected the width of the 95% confidence interval for the Schnabel model (y=50.79-2.016x, $F_{1,10}$ =5.669, P<0.0001; Fig. 4.5 f). For all the other models the width of the confidence limits did not change with increased sighting effort (negative binomial, y=89.31-2.534x, $F_{1,10}$=0.93, P=0.357, Poisson, y=28.98+0.227x, $F_{1,10}$=3.50, P=0.091, Bowden's, y=17.46-0.041, $F_{1,12}$=0.08, P=0.776, Jolly-Seber, y=17.74+3.995x $F_{1,10}$=2.01, P=0.199, Schumacher, y=23.35-0.535x, $F_{1,10}$=1.06, P=0.327; Fig. 4.5 a-e).

For breeding herd observations during resighting events the width of the 95% confidence interval also showed no significant improvement with increased effort over time (y=75.40-1.330x, r^2=0.09, $F_{1,5}$=0.51, P=0.509; Fig. 4.6a). However, when lumping the data for all breeding herds the width of the 95% confidence interval decreased significantly with increasing sampling effort (number of sightings)(y=146.70-2.315x, r^2=0.58, $F_{1,35}$=72.94, P<0.0001; Fig. 4.6b).

Evaluation of resight models

Based on the Akaike information criterion (AIC_c) the Bowden's model (AIC_c=0.87) is the most suitable when sample sizes are small. This is followed by the Schnabel (AIC_c=0.10), Schumacher (AIC_c=0.03) and Poisson (AIC_c=0.01) models. The Jolly-Seber (AIC_c=0.00) and negative binomial (AIC_c=0.00) models were the least suitable of the models I evaluated. The factors which have the largest impact on model suitability, when viewed across all models are that all animals have the same probability of sighting in the first sample, marks are not lost, marking does not affect catchability and that the population is closed.

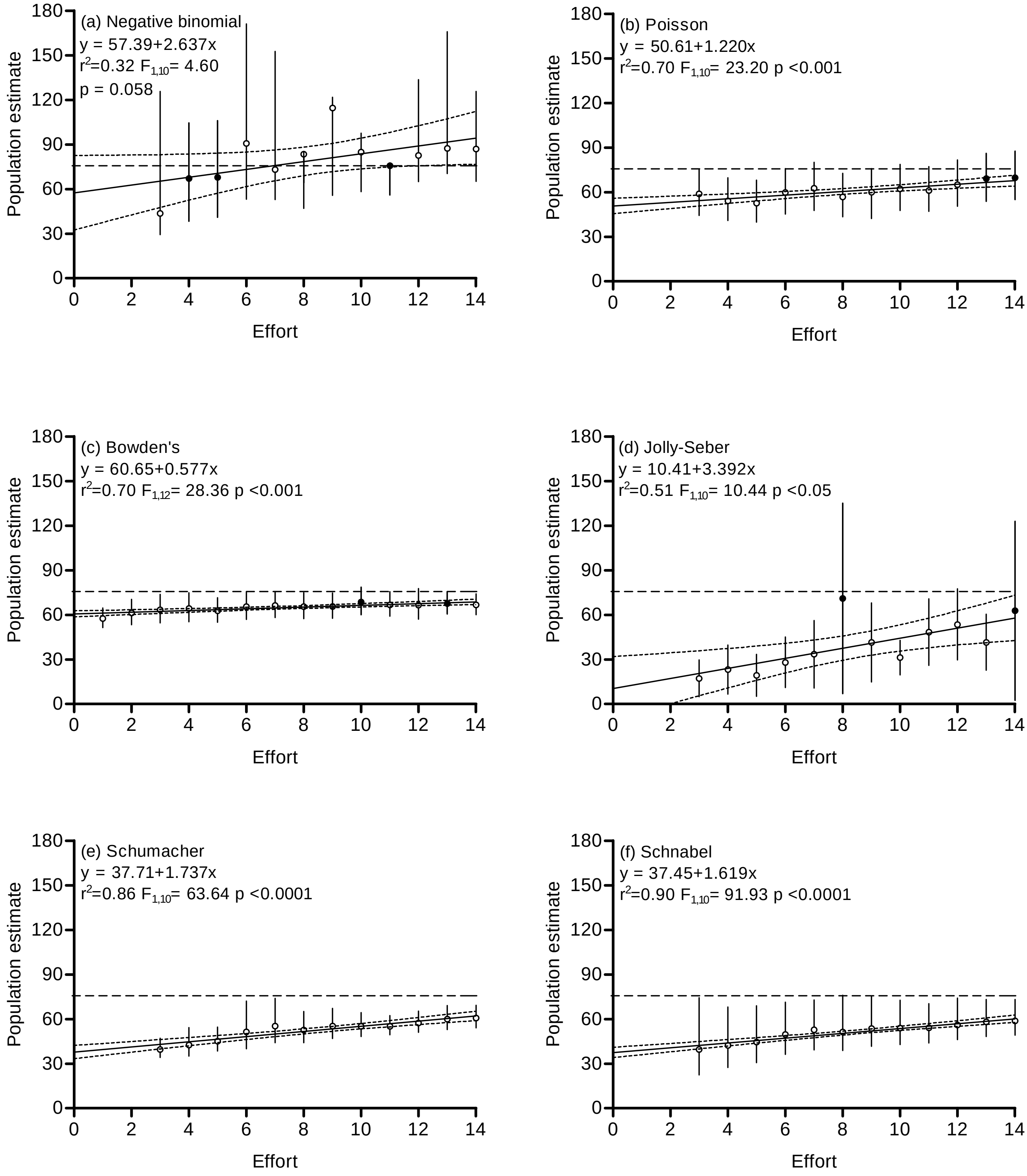
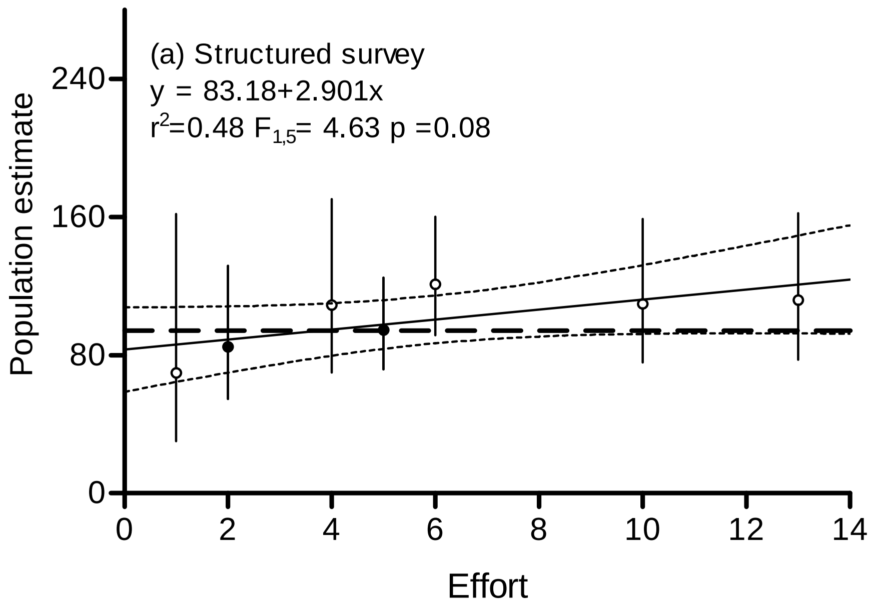


Figure 4.3. Legend on next page.

Figure 4.3. The influence of survey effort on population estimates for bulls from sight-resight models over 14 sighting events. Points indicate population estimate and vertical lines denote the 95% confidence intervals. Solid points indicate estimates that are within ten percent of the registration count (dashed horizontal line). Solid diagonals are regression lines fitted through least squares regression analysis and dotted lines are their 95% confidence intervals. The F-values test for deviation from zero of the slopes of the regression lines.



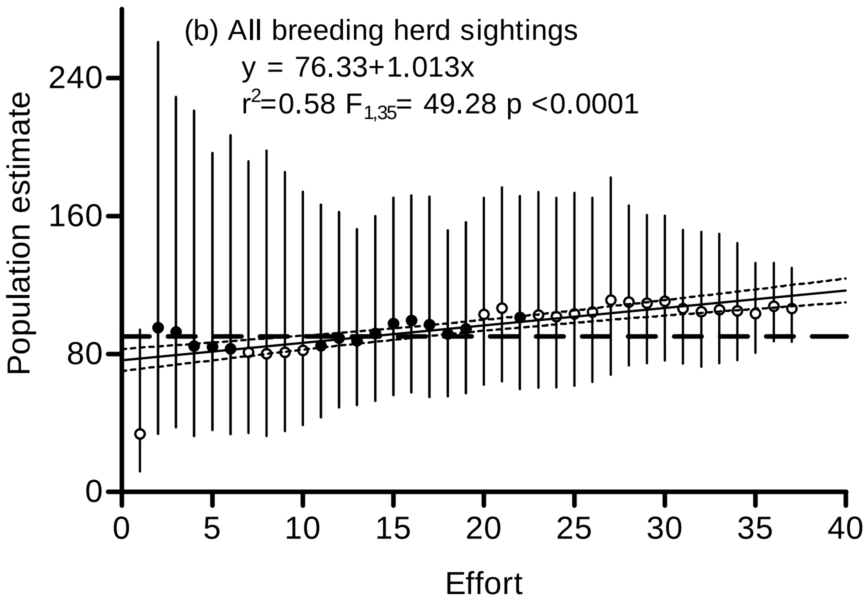


Figure 4.4. The influence of survey effort on population estimates for elephants in breeding herds using the Bowden's estimator for (a) 14 resighting sessions on structured surveys and (b) for all post-marking sightings of breeding herds. Circles indicate population estimates. Solid circles are within 10% of the registration count (dashed horizontal line). Vertical lines indicate 95% confidence intervals of the population estimates. Regression lines were fitted through least square regression analysis (dotted lines present the 95% confidence intervals). The F-values test for deviation from zero of the slopes of the regression lines.

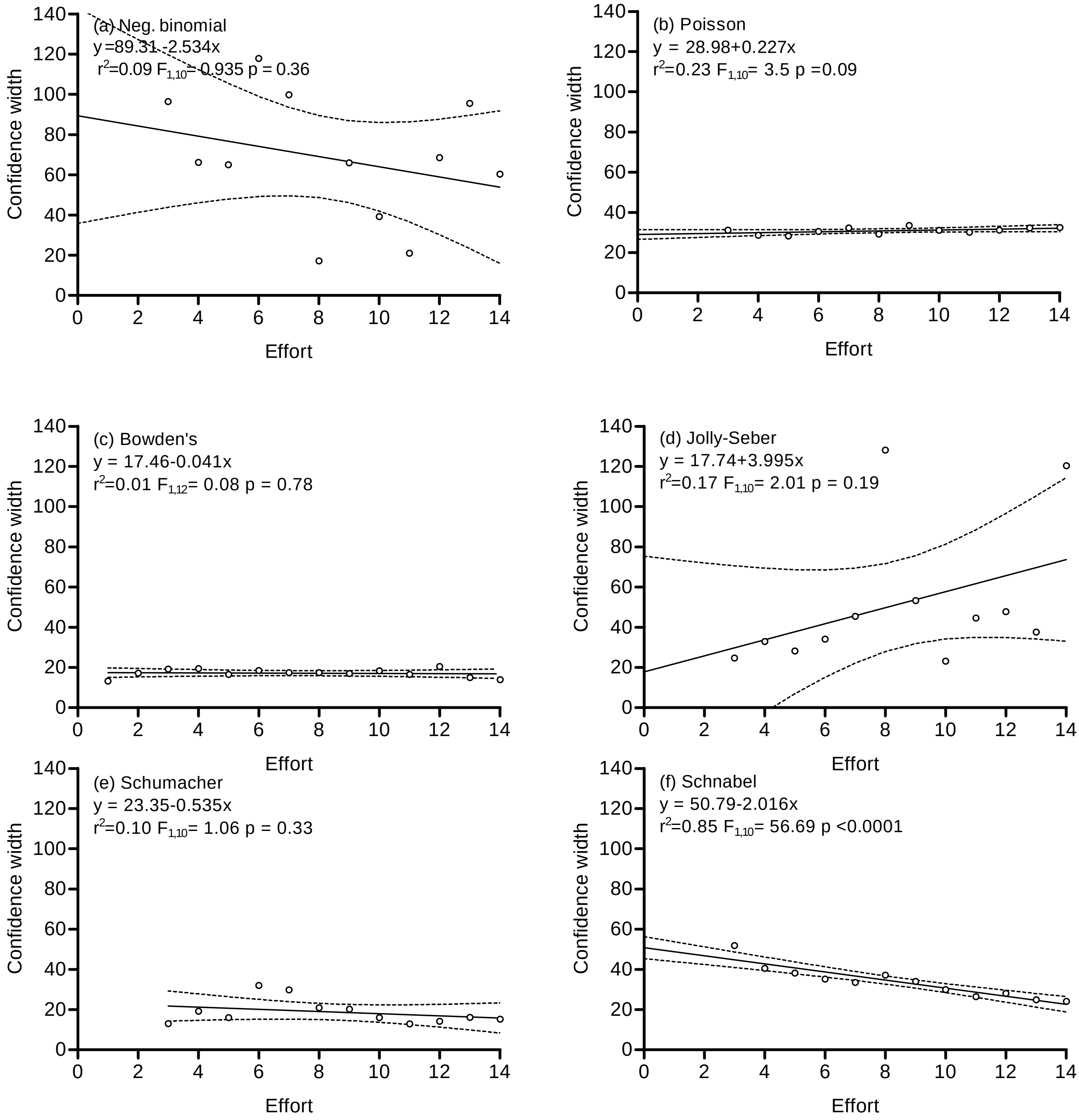


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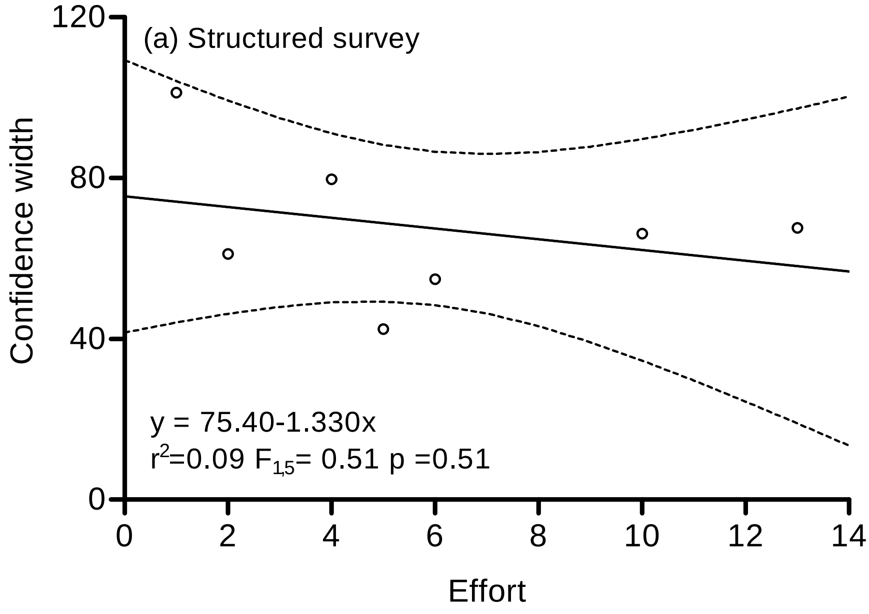
Figure 4.5. The influence of sampling effort on the width of the confidence limits of estimates of population size for bulls. Least squares linear regression analyses were used to evaluate change in the 95% confidence intervals for sight-resight models as effort increased through the number of resighting sessions. Models are (a) negative binomial, (b) Poisson, (c) Bowden's, (d) Jolly-Seber, (e) Schumacher and (f) Schnabel.



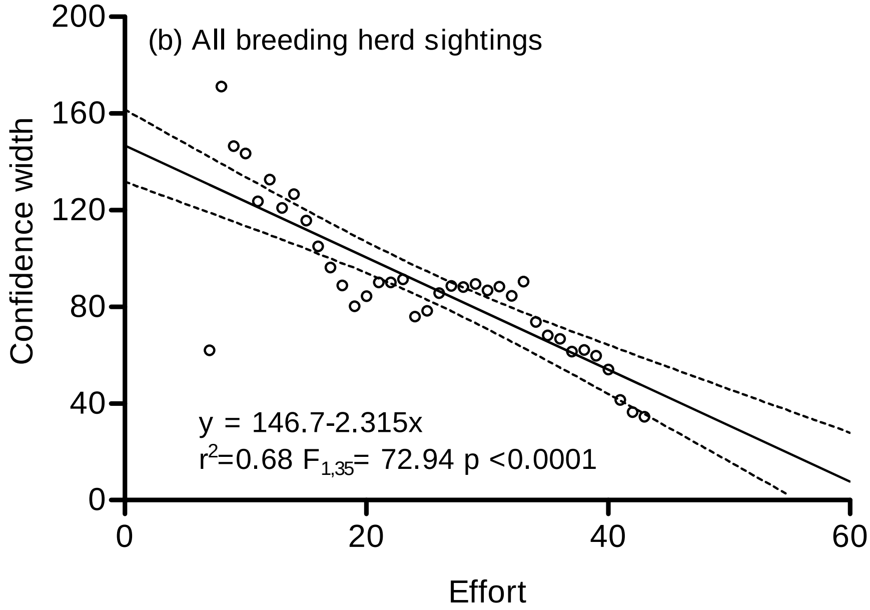


Figure 4.6. The influence of sampling effort on the width of the confidence limits of estimates of population size for elephants in breeding herds. Figures show least squares linear regression analysis of 95% confidence intervals for breeding herds for the Bowden's estimator, where (a) effort constitutes 14 resighting sessions and (b) effort comprises of all post-marking sightings of breeding herds.

Discussion

Capture-recapture models often are used to estimate abundances (e.g. Krebs 1999; Nichols 1992; Pollock 1991, 2000; Pollock *et al*. 1990; Seber 1982, 1986, 1992 and references therein). These models have been used to estimate abundance for a wide range of large mammals including bottle nose dolphins *Turslops truncatus* (Wilson, Hammond & Thompson 1999), bison *Bison bison* (Minta & Mangel 1989), tigers *Panthera tigris* (Karanth & Nichols 1998), mountain sheep *Ovis canadensis* (Neal *et al*. 1993) and moose *Alces alces shirasi* (Bowden & Kufeld 1995), but have not been applied to elephants.

This study suggests that some mark-resight models may yield population estimates similar to those derived from registration counts for a closed population of elephants. Model selection, however, is important as the violation of assumptions reduce their utility. Such methods may still be better than enumeration methods because mark-resight models are less biased than those based on the minimum-number-alive method (Krebs 1999).

A zero-truncated poisson test (see Krebs 1999) indicated that for elephant bulls the assumption of equal catchability was violated in my study, this compromised five of the eight models used (Table 4.1). The Jolly-Seber model proved least effective because it is specifically designed for open populations and where catchability is equal (Krebs 1999). It yielded wide confidence intervals that did not improve with increased effort. The Petersen model was the simplest model I tested and the low number of sightings and subsequent resightings could have compromised the model's performance, as could its sensitivity to unequal catchability (see Minta & Mangel 1989; Seber 1992). The negative binomial model was the only model I used that produced an estimate higher than the registration counts. The remaining models all produced estimates lower than the known population size but with confidence limits that were closer to the minimum number known to be present through registration counts. All the models I used yielded estimates closer to the known population than the aerial surveys. The Bowden's estimator, Schumacher method and the Schnabel method provided underestimates of the registration count at the upper 95% confidence limit although these were small.

For breeding herds my estimate of population size using the Bowden's estimator exceeded the registration count, though the lower confidence limit included the known population estimate. The estimate of total population size (bulls and breeding herds) from the Bowden's estimator, derived from resighting sessions, is close to the registration count and precision improved when I included all post-marking observations. This method yielded an estimate in which the 95% confidence intervals overlapped the registration count. My estimates of total population size from the Bowden's estimator are closer to the number of elephants known to be present in the area than those yielded by aerial surveys. The Bowden's estimator allowed me to use all sightings of marked animals, which, in the case of the breeding herds improved precision (a narrower confidence limit) although the estimate of population size was similar.

The effort expended on sighting sessions is important when designing a mark-resight study. For the breeding herds, the number of observations during sighting sessions was insufficient to provide a significant improvement in the population estimate and confidence interval. With increased effort both population estimates and confidence intervals improved significantly. For bulls all the models tested with the exception of the negative binomial estimate, showed an increased precision with increasing effort. Only the Schnabel model showed a significant narrowing in confidence interval with increased effort over 14 sighting sessions.

Of the models tested, the Bowden's estimator was the most suitable model for determining population size under the conditions prevailing during my study. The Bowden's estimator showed the highest probability that it was the best model of those selected (AIC_c weight), and is designed for closed populations. The model's ability to function without an assumption of equal catchability is a key attribute, and it was the only model tested that is not dependent on all marks being recorded in subsequent recapture (resighting) events. It therefore was the only model that could be applied to the breeding herd in the population. While the precision of estimates did not improve with increased effort for the bulls, for the breeding herds the precision of the estimate did improve with increased effort (number of observations). The Petersen, Schumacher and Schnabel models are dependent on an assumption of equal catchability and could be compromised by the violation of this assumption in this study. The Petersen model was the simplest model tested and relies on a single marking event and a single recapture event. It yielded a population estimate (38 bulls) far below the registration count (75 bulls). The only model tested that showed an increase in the precision of the population estimate with increased effort was the Schnabel model.

The Poisson, Robust and negative binomial and Schnabel models are designed for open populations. Of these models only the Poisson assumes equal catchability. As could be expected the least applicable model for this closed population was the Jolly-Seber. The Jolly-Seber model is specifically designed for open populations and is highly sensitive to violations of the assumption of equal catchability. Although the estimate of population size (63 bulls) was within the range of other models tested

(Petersen = 38 bulls to negative binomial = 87 bulls), model evaluation using AIC_c showed it to be an unsuitable model. The negative binomial model was the only model that did not show an improved 'match' to the registration count with increased effort.

Previous estimates of population size for elephants in the TEP using aerial survey methods yielded under estimates. As a result of small population size too few observations were obtained to allow the calculation of confidence intervals (Matthews 2000). Aerial survey methods are relatively expensive and reliant on specialist staff. Mark-resight surveys also are expensive and time intensive to initiate but once the initial survey has been conducted subsequent estimates can be more cost effective (Minta & Mangel 1989). Conservation organizations in Africa have to compete for funding with other agencies and financial resources are limited so cost efficient methods are vital.

I show that for small, closed elephant populations such as that of TEP estimates of population size based on mark-resight estimates are valid with confidence intervals narrower than those reported for dung counts elsewhere. Where population estimates have been determined from dung counts investigators often failed to calculate mean decay rate or mean defecation rate, therefore their estimates are unreliable (Nchanji & Plumptre 2001; Barnes 2002). Where defecation and decay rates were determined, confidence intervals are wide (see Barnes & Dunn 2002).

Population counts based on the individual identification of elephants have assumed all elephants in the populations are known (Whitehouse & Hall-Martin 2000; Moss 2001) and no confidence intervals are obtained. These estimates are based on long-term studies conducted over about 30 years (Moss 2001) and 70 years (Whitehouse & Hall-Martin 2000), and therefore not applicable to most populations.

It has recently been proposed that the monitoring of vocal communication between elephants is a potential method of estimating population size (McComb *et al*. 2003; Payne, Thompson & Kramer 2003). At present, however, these methods work over short distances and do not reliably identify individuals (McComb *et al*. 2003). Currently methods based on vocal communication are experimental and are not yet suitable for estimating population size for elephants (see Payne *et al*. 2003).

Aerial surveys are widely used to estimate elephant populations (see Blanc *et al*. 2003), although shortcomings have been identified (see Caughley 1974; Pollock & Kendall 1987; Jachmann 2002; Khaemba & Stein 2002). Aerial surveys of small populations living in forests or thickets yield questionable estimates of population size (Whitehouse *et al*. 2001; Barnes 2002).

Few aerial surveys conducted in central, southern and east Africa report confidence intervals. Even in the Kruger National Park, where aerial surveys have been conducted yearly since 1967, confidence intervals are not derived for population estimates.

Repeated mark-resight surveys can yield population trends for closed populations. A complete mark-resight survey for reserves similar in size to TEP could be completed in eight to ten days. Once established, three to four resight surveys per year would be sufficient to monitor population size and could be maintained by non-specialist technical staff.

The population estimates I derived from Bowden's estimator (N=179, 95% CI=136-233), show that given the difficulties associated with alternative methods of estimating abundance for savanna elephant populations under conditions such as those prevailing in the TEP, mark-resight methods are an alternative to methods of enumeration more commonly used.