Title: Optimal sampling frequency and timing of threatened tropical bird populations: a modeling approach

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Conservation of threatened or endangered species relies critically on accurate population counts over time. In practice, many population censuses are conducted by non-governmental organizations or volunteer citizen scientists who are constrained by fiscal and temporal resources. Less than optimal sampling regimens (including frequency and timing) for conducting population censuses can result in woefully misleading population estimates - and thus have dire consequences for management and conservation. Motivated by an East African case study in which we parameterized a Leslie matrix model with nearly 15 years of bird data collected in the Arabuko-Sokoke Forest in coastal Kenya, we carried out mathematical and statistical modeling efforts with the Leslie models for simulated population estimates stemming from different population sampling schemes. We illustrate how resource managers might take a strategic approach, using simple quantitative models, to develop an optimal sampling scheme that balances the tradeoff between resources and accuracy.

Introduction

Conservation science in practice is often constrained by resource availability, which has implications for data analysis and interpretation as well as management. Underpinning most conservation efforts, from local volunteer programs to large-scale population viability analyses, is an ongoing need to characterize population abundance and diversity based on population census counts (Simberloff 1988; Brook et al. 2000; Morris and Doak 2002; Karanth et al. 2003). Scarcity of resources often necessitates making difficult decisions about how often and when to collect data. Although amassing as much data as possible is of course generally recommended, many factors, (including some biotic and abiotic factors such as weather conditions that are unrelated to resources) often conspire to prevent frequent and regular sampling of population abundance or diversity. A lack of resources often translates into data that are collected in a haphazard manner, with gaps in data collection during critical times in the life history of species being studied. Resulting poor quality data sets can lead to misleading population estimates and risk assessment (Holmes 2001).

Bird counts provide an excellent means of illustrating the tradeoffs and nuances involved in the frequency and timing of data collection. Many bird population estimates rely on the efforts of local non-governmental agencies or citizen-science groups, or other volunteer organizations (Newson et al. 2005; Freeman et al. 2007). Coordinated long-term datasets, such as those generated by Christmas Bird Counts (Link et al. 2006) or the North American Breeding Bird Survey (Kendall et al. 1996) strive to maintain consistency in both the timing and regularity of sampling. In contrast, other less coordinated efforts, especially those done at a small local scale, are often conducted inconsistently with little regularity due to meager personnel resources. In the tropics, these activities often fall to non-governmental organizations (NGOs) and non-profits with uncertain or ephemeral funding sources, which can result in inconsistent sampling frequencies and timing.

We describe here a case study stemming from bird count data collected by staff and citizen-science volunteers from A Rocha Kenya at the Mwamba Field Studies Centre, a non-profit conservation group in Watamu, Kenya. In particular, we use this case study to develop a methodology for determining the optimal sampling scheme to accurately estimate populations of a threatened bird population given limited monitoring resources. Motivated by nearly 15 years of population census counts of the East Coast Akalat, an Old World flycatcher in coastal Kenya, we employ a combined mathematical and statistical modeling approach to determine the optimal frequency and seasonal timing of mist-net capture sessions. Mist netting is a common means of sampling bird populations, and while some studies have suggested it is not an optimal technique for comparing species abundance across habitats (Remsen and Good 1996), it has been shown to be more accurate than point counts in estimating population abundance when employed in breeding habitats (Rappole et al. 1993). We explore the accuracy of several different sampling strategies and discuss implications for conservation in practice.

Materials and methods

Study organism/site

The East Coast Akalat (*Sheppardia gunningi sokokensis* Haagner) is a small forest robin that is restricted to small coastal forests in East Africa (Matiku et al. 2000). Distributed among remnant forest patches, *S. gunningi* is vulnerable to continuing habitat threats such as logging and development and has been classified as near threatened (declining population trend) by the

World Conservation Union (IUCN 2014). Formerly abundant along the east African coast from Kenya to Malawi and Mozambique, *S. gunningi* is now found primarily in the coastal forests of Kenya, with the largest remnant population (approx. 7500 pairs) residing year-round in Arabuko-Sokoke Forest (ASF), a 429km^2 forest reserve that is the largest remnant patch of indigenous coastal forest in East Africa (Bennun and Njoroge 1999; Birdlife International 2008; Banks et al. 2012). Because *S. gunningi* co-occurs with several other highly endangered and rare species, including several other bird species as well as the Sokoke Bushy-tailed Mongoose, Aders' Duiker, and Golden-rumped Elephant Shrew, it has become an indicator species for habitat conservation efforts in the Arabuko-Sokoke Forest reserve.

Data collection

S. gunningi individuals were collected in mist nets by staff from the Mwamba Field Studies Centre/A Rocha Kenya in an area in the north-eastern corner of Arabuko-Sokoke Forest known as the Gede Nature Trail from 1999-2012. Standard mist netting protocols were followed: for each session, total net lengths measured 180m and samples consisted of captures from two consecutive dawn capture periods. After removal from the net, plumage characteristics, molt pattern, and age and sex were recorded for each akalat, and bands were placed on birds that were not recaptures. Akalats were categorized, where possible, into one of three age classes: immature, subadult, or full adult. In cases where a clear designation was not possible, birds were categorized initially as "unknown age". Birds were captured in 24 sessions over 14 years, at non-uniform time intervals with consistent ringing effort. The number of sampling sessions per year ranged from zero to eight, with a mean of approximately two. Data consisting of the number of akalats in each age class for each mist-netting session (see Appendix I) were then incorporated into a predictive population model. In five of the ringing sessions, some captured birds were difficult to age because they were at a transitional stage – these birds were added to the "full adult" category based on the time of year when they were captured and the likelihood that they were subadults transitioning to full adults.

Mathematical Model

We incorporated life history data into a Leslie matrix mathematical model (Leslie 1945) to generate *S. gunningi* population projections for the 13 year sampling period. The number of individuals in each of the three stage classes is denoted by x_i for $i = 1, 2, 3$, with the population expressed as a vector $\mathbf{X} = [x_1, x_2, x_3]^T$. Then the population growth may be described by the mathematical model:

$$\mathbf{X}(t+1) = \begin{bmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{bmatrix} = \begin{bmatrix} 0 & 0 & F_3 \\ G_1 & 0 & 0 \\ 0 & G_2 & P_3 \end{bmatrix} \begin{bmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \end{bmatrix} = \boldsymbol{f}\left(\mathbf{X}(t), \mathbf{q}\right) = \mathbf{A}\,(\boldsymbol{q})\,\mathbf{X}(t) \qquad \text{(Eqn. 1)}$$

where the G_i and P_i and represent the rate of individuals surviving from the i^{th} to the $(i+1)^{st}$ stage ($0 < G_i < 1, i = 1,2$ and $0 \le P_3 < 1$), F_3 denotes the reproductive rate of full adults (3rd life stage), and *t* is given in months.

Statistical Models & Parameter Estimation

Creating population projections using this model requires us to estimate the four life history parameters; in notation, we refer to a vector containing the parameters in the above matrix (Eqn. 1). Let $\boldsymbol{q} = [F_3, G_1, G_2, P_3]$ in which the four parameters are as above, and are assumed to be in an admissible constraint set Q_{AD} that reflects all reasonable values of fecundity and survivorship for *S. gunningi*. We accomplished this by performing a least squares optimization using the data collected by A Rocha Kenya. We estimated the *S. gunningi* fecundity rate by noting that an average clutch size for similar birds is roughly 3-5 eggs and halving this to reflect the fact that only females breed; thus we initially let $F_3 = 2$ and only estimated (G_1, G_2, P_3). Because they are probabilities, survivorship parameters (G_1, G_2, P_3) were constrained to lie between 0 and 1. With a broad spectrum of initial guesses within the admissible range of parameter values, we then solved the inverse problem using least squares optimization in order to generate optimal parameter values (see Banks and Tran 2009; Banks et al. 2013 for more details). The general form of this solution minimizes the discrepancy between the data and the model output of all possible vectors containing the life history parameters **q.** This may be described for *n* observations by the following expression:

$$\mathbf{q}_{OLS}(\boldsymbol{Y}) = \arg\min \sum_{k=1}^{n} [\mathbf{Y}_k - \boldsymbol{f}\left(\mathbf{X}(t_k), \mathbf{q}\right)]^2 \qquad \text{(Eqn. 2)}$$

where $\boldsymbol{Y}_k$ denotes the data, and $\boldsymbol{f}$ denotes the model (as a function of time and the life history parameters in the vector $\boldsymbol{q}$). We note that this formulation is based on an assumed statistical model $\boldsymbol{Y}_k = \boldsymbol{f}(\mathbf{X}(t_k), \boldsymbol{q}_0), + \boldsymbol{E}_k$, where $\boldsymbol{q}_0$ is an assumed true parameter and the errors $\boldsymbol{E}_k$ for $k = 1, \ldots, n$ are independent identically distributed random variables (see Banks and Tran 2009 for details).

Because juvenile birds are less likely to be captured in mist nets than adults, we modified our model assumptions. In particular, we modified the least squares formulation to reflect the fact that one age class of data (full adults) was expected to be subject to less observation error than the other two classes, giving more weight to the full adult data points than to the immature or subadult points when searching for optimal parameters.

The functional that we minimize in this case is thus modified by weighting as follows:

$$\boldsymbol{q}_{WLS}(\boldsymbol{Y}) = \arg\min \sum_{k=1}^{n} w_1[Y_{1,k} - f_1\left(\mathbf{X}(t_k), \boldsymbol{q}\right)]^2 + w_2\left[Y_{2,k} - f_2\left(\mathbf{X}(t_k), \boldsymbol{q}\right)\right]^2 + w_3\left[Y_{3,k} - f_3\left(\mathbf{X}(t_k), \boldsymbol{q}\right)\right]^2$$

(Eqn. 3)

where we weighted each age class in increasing order from youngest to oldest. This corresponds to a statistical model $\boldsymbol{Y}_k = \boldsymbol{f}\left(\mathbf{X}(t_k), \mathbf{q}_0\right) + \mathbf{V}\,\boldsymbol{E}_k$ where $\mathbf{V} = \mathbf{diag}(1/w_1, 1/w_2, 1/w_3)$, with w_1, w_2 and w_3 corresponding to immatures, subadults, and full adults, respectively. The weighted least squares method can be particularly advantageous over the ordinary least squares method when one class of data is known to have greater error than others (Banks and Tran 2009). Therefore, the appropriate method to use is highly dependent on the data at hand. With both ordinary and weighted least squares estimates, one can calculate the standard variance and underlying distribution of each parameter by employing bootstrapping (see Banks et al. 2009, and Banks et al. 2013 for examples). In studying the *S. gunningi* data, we found there appeared to be relatively high error in the data collection process. More importantly, the *irregularity* with which the data was collected was striking. Motivated by these observations, we turned to the more important fundamental question: Given limited resources that that may be inherent, how should one best collect data in order to validate a given class of models. For these investigations we choose the Leslie matrix models that we had been using in our Akalat studies.

Simulation-Based Experimental Design

We thus turned to the question of how the population is projected to grow or decrease over time. Our fundamental question was thus the following: *with the limited resources of small non-profit* *organizations such as A Rocha Kenya that are engaged in many conservation efforts globally, what is the optimal yearly data collection schedule that is both realistic given resource constraints and sufficient to demonstrate population dynamics?* Choosing a parameter set $\boldsymbol{q}$ = [2, 0.3, 0.8, 0.9] (which was chosen given knowledge of similar species and our previous analysis of the akalat data), we used the matrix model to generate population values for each month for five years (12 sessions per year times 5 years = 60) by repeatedly multiplying the transition matrix (**A**) and each successive population vector (with the initial population vector fixed at $\boldsymbol{X_0}$ = [1, 1, 2], reflecting the average number of akalats caught per session and the ratio among age classes).

From this simulated data set, we then compared life history parameter estimates generated from four different sampling schemes. For the effort we report on here, we used ordinary least squares estimation (although similar results were found using weighted least squares.) Rather than present an exhaustive list of all possible sampling schemes, we describe the results stemming from several illustrative and contrasting combinations of sampling schemes. The schemes we report on are (1) sampling each month for the entire five years, (2) sampling four months each year during January, April, July and October, which includes one sample during the breeding season, (3) sampling four months each year during January, February, March and December, which includes two samples during the breeding season, and (4) sampling four months each year during May, July, September and November that excludes sampling during the breeding season.

In order to quantify which sampling scheme gives us the most accurate fit to the actual population size (which is known, as it was simulated using the fixed life history parameter values), we again solved the inverse problem based on simulated data for each sampling scheme. We compared the schemes (2), (3), and (4) to the actual simulated data by examining how closely the solution to the inverse problem recovered the original life history parameters (see Banks et al. 2013 for more details).

Results

The solution to the inverse problem with no error in the statistical model generated, as expected, an initial vector of life history values of $\boldsymbol{q} = [2.0, 0.3, 0.8, 0.9]$. Population projections for the baseline monthly sampling scheme across five years generated cyclical peaks accurately reflecting the akalat breeding season (Figure 1). However, the other sampling schemes had varying success (Table 1) in capturing these akalat population dynamics broken down by life stage. Samples during four months per year that included one breeding sample (Figure 2) resulted in a close match to the original population trajectories stemming from five years' simulated data. The scheme that included two breeding season samples was slightly less accurate (Figure 3), with less distinct peaks and troughs, especially for immature and full adult akalats (Figure 3a, c). The scheme that excluded any breeding season samples fared much worse, especially for immature and sub-adult dynamics (Figure 4). Overall, four monthly samples per year including one breeding season in the sample resulted in the best parameter recapture and lowest cost functional of the three options when compared with the baseline simulated data (Table 1). These results were consistent with those obtained when we carried out the same estimation procedures with different levels of noise in the statistical models.

Discussion

The importance of accurate population estimates in conservation science cannot be overstated. Failure to detect dynamics accurately can lead to overoptimistic assessments of how populations are faring, which can have disastrous consequences for management (Gilroy et al. 2012). In many tropical conservation settings, population census efforts are severely restricted due to underfunding or insufficient personnel and resources. These challenges are exacerbated by the fact that population counts are often done by ephemeral initiatives and oft-changing staff at non-profit NGOs – so that both sampling frequency and timing are inconsistent. In the current exercise we used population counts for a near threatened bird endemic to East Africa to highlight features of sampling schemes critically important for accurately assessing population dynamics given constrained resources. Our results highlight the need to establish regular, consistent sampling schemes to establish accurate bird population counts – with special attention given to including at least one sample during the breeding season. This may present special challenges for planning population counts of tropical birds such as *S. gunningi*, as the breeding season in tropical birds is notoriously narrower and less predictable than temperate birds (Stauffer et al. 2013). Other recent ornithological studies have shown that multiple sampling periods within the year generally produce more accurate results, especially with respect to reproductive output (e.g., Betts et al. 2004).

Several complicating factors are worth noting in interpreting the results of this simple modeling exercise. First, aging birds is an imperfect process, with much uncertainty due to both observation and sampling error. In a few exceptional cases, clear correlates have been identified among traits such as wing color, age, and reproductive potential (Blanco and Fargallo 2013). In the current exercise we made some simple assumptions regarding the handful of birds that we captured that proved difficult to age. However, much more emphasis needs to be placed on developing accurate, dependable methods of precisely determining age.

Second, better information on life history ecology, dispersal and/or recruitment rates, and other ecological attributes of rare or endangered species are needed to generate more accurate predictions of population growth/dynamics in the long term (Clark and Martin 2007; Hernández-Matías et al. 2013). For birds such as *S. gunningi*, this will require much more intensive study and focus – a challenge for activities in important sites such as the Arabuko-Sokoke Forest and other underfunded conservation efforts.

Finally, some aspects of the matrix mathematical model formulation presented here may heavily influence outcomes and interpretation. In the present model, we used constant estimates for the vital rates to generate population projections, which ignores potentially complex shifting conditions likely to be influential drivers of survivorship and fecundity through time (Caswell 2001; Gotelli and Ellison 2006). A different approach worth considering would be to use a model incorporating time-varying vital rates (e.g., Banks et al. 2008). Furthermore, Yearsley (2004) cautions that ignoring the initial population structure may result in unreliable short-term or transient population dynamics assessments in demographic analyses using matrix models. Although we focus here on long-term asymptotic outcomes, it is worth noting the importance of accurate parameter estimation in seeding such models. Overall, however, our results should prove to be generalizable to diverse taxa in both tropical and temperate ecosystems.

Acknowledgments

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Literature Cited

Banks HT, Banks JE, Jackson C, Rinnavotore K (2013) Modeling the East Coast Akalat population: Model comparison and parameter estimation. Center for Research in Scientific Computation Technical Report, North Carolina State University. CRSC-TR13-12.

Banks HT, Tran HT (2009) Mathematical and Experimental Modeling of Physical and Biological Processes. CRC Press, Boca Raton, FL.

Banks JE, Dick LK, Banks HT, Stark JD (2008) Time-varying vital rates in ecotoxicology: selective pesticides and aphid population dynamics. Ecol Model 210: 155-160.

Banks JE, Jackson CM, Baya A, Minella H, Nitz M, Hitchcock J, Bruinsma D (2012) Forest type preference of an Afrotropical thrush (East Coast Akalat, *Sheppardia gunningi sokokensis*) in Arabuko-Sokoke Forest, Kenya. Ostrich 83: 105-108.

Banks HT, Holm K, Robbins D (2009) Standard error computations for uncertainty quantification in inverse problems: Asymptotic theory vs. Bootstrapping. Math Comp Model 52: 1610-1625.

Bennun L, Njoroge P (1999) Important bird areas in Kenya. Nairobi: East Africa Natural History Society.

Betts MG, Simon NPP, Nocera JJ (2004) Point count summary statistics differentially predict reproductive activity in bird-habitat relationship studies. J Ornith 146: 151-159.

Birdlife International (2008) East Coast Akalat. BirdLife Species Fact Sheet. Available at www.birdlife.org. Accessed 30 January 2014.

Blanco G, Fargallo JA (2013) Wing whiteness as an indicator of age, immunocompetence, and testis size in the Eurasian Black-Billed Magpie (*Pica pica*). Auk 130: 399-407.

Brook BW, O'Grady JJ, Chapman AP, Burgman MA, Akçakaya HR, Frankham R (2000) Predictive accuracy of population viability analysis in conservation biology. Nature 404: 385-387.

Caswell H (2001) Matrix Population Models: Construction, Analysis, and Interpretation, second ed. Sinauer, Sunderland, MA.

Clark ME, Martin TE (2007) Modeling tradeoffs in avian life history traits and consequences for population growth. Ecol Model 209: 110-120.

Freeman SN, Noble DG, Newson SE, Baillie SR (2007) Modelling population changes using data from different surveys: the Common Birds Census and the Breeding Bird Survey. Bird Study 54: 61-72.

Gilroy JR, Virzi T, Boulton RL, Lockwood JL (2012) Too few data and not enough time: approaches to detecting Allee effects in threatened species. Cons Lett 5: 313-322.

Gotelli N, Ellison A (2006) Forecasting extinction risk with nonstationary matrix models. Ecol Appl 16: 51–61.

Hernández-Matías A, Real J, Moleón M., Palma L., Sánchez-Zapata JA, Pradel R, Carrete M, Gil-Sánchez JM, Beja P, Balbontín J, Vincent-Martin N, Ravayrol A, Benítez JR, Arroyo B, Fernández C, Ferreiro E, García J (2013) From local monitoring to a broad-scale viability assessment: a case study for the Bonelli's Eagle in western Europe. Ecol Monogr 83: 239-261.

Holmes EE (2001) Estimating risks in declining populations with poor data. Proc Nat Acad Sci USA 98: 5072-5077.

IUCN (International Union for the Conservation of Nature) (2012) Available at www.iucnredlist.org. Accessed 30 January 2014.

Karanth KU, Nichols JD, Seidenstricker J, Dinerstein E, Smith JLD, McDougal C, Johnsingh AJT, Chundawat RS, Thapar V (2003) Science deficiency in conservation practice: the monitoring of tiger populations in India. Anim Conserv 6: 141–146.

Kendall WL, Peterjohn BG, Sauer JR (1996) First-time observer effects in the North American Breeding Bird Survey. Auk 113: 823-829.

Leslie PH (1945) On the use of matrices in certain population dynamics. Biometrika 33: 184-212.

Link WA, Sauer JR, Niven DK (2006) A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. Condor 108: 13-24.

Matiku PM, Bennun LA, Nemeth E (2000) Distribution and population size of the threatened East Coast Akalat in Arabuko-Sokoke Forest, Kenya. Ostrich 71: 282-285.

Morris WF, Doak DF (2002) Quantitative Conservation Biology: Theory and Practice of Population Viability Models. Sinauaer Associates, Inc., Sunderland, MA.

Newson SE, Woodburn RJW, Noble DG, Baillie SR, Gregory RD (2005) Evaluating the Breeding Bird Survey for producing national population size and density estimates. Bird Study 52: 42-54.

Rappole JH, McShea WJ, Vega-Rivera J (1993) Evaluation of two survey methods in upland avian breeding communities. J Field Ornith 64: 55-70.

Remsen JV, Good DA (1996) Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113: 281-298.

Simberloff D (1988) The contribution of population and community biology to conservation science. Annu Rev Ecol Evol 19: 473-511.

Stouffer PC, Johnson EI, Bierregaard RO Jr (2013) Breeding seasonality in central Amazonian rainforest birds. Auk 130: 529-540.

Yearsley JM (2004) Transient population dynamics and short-term sensitivity analysis of matrix population models. Ecol Model 177: 245-258.

FIGURE LEGENDS:

Figure 1. Simulated akalat population size for monthly samples over five years for (a) immature, (b) sub-adult, and (c) full adult akalats.

Figure 2. Simulated akalat population size for four monthly samples per year over five years including one breeding sample for (a) immature, (b) sub-adult, and (c) full adult akalats.

Figure 3. Simulated akalat population size for four monthly samples per year over five years including two breeding samples for (a) immature, (b) sub-adult, and (c) full adult akalats.

Figure 4. Simulated akalat population size for four monthly samples per year over five years including no breeding samples for (a) immature, (b) sub-adult, and (c) full adult akalats.

References

Banks HT, Banks JE, Jackson C, Rinnavotore K (2013) Modeling the East Coast Akalat population: Model comparison and parameter estimation. Center for Research in Scientific Computation Technical Report, North Carolina State University. CRSC-TR13-12.

Banks HT, Tran HT (2009) Mathematical and Experimental Modeling of Physical and Biological Processes. CRC Press, Boca Raton, FL.

Banks JE, Dick LK, Banks HT, Stark JD (2008) Time-varying vital rates in ecotoxicology: selective pesticides and aphid population dynamics. Ecol Model 210: 155-160.

Banks JE, Jackson CM, Baya A, Minella H, Nitz M, Hitchcock J, Bruinsma D (2012) Forest type preference of an Afrotropical thrush (East Coast Akalat, *Sheppardia gunningi sokokensis*) in Arabuko-Sokoke Forest, Kenya. Ostrich 83: 105-108.

Banks, H.T., Holm, K. & Robbins, D. (2009). Standard error computations for uncertainty quantification in inverse problems: Asymptotic theory vs. Bootstrapping. *Math Comp Model*, **52**, 1610-1625.

Bennun, L. & Njoroge, P. (1999). Important bird areas in Kenya. Nairobi: East Africa Natural History Society.

Betts, M.G., Simon, N.P.P. & Nocera, J.J. (2004). Point count summary statistics differentially predict reproductive activity in bird-habitat relationship studies. *J Ornithol*, **146**, 151-159.

Birdlife International. 2008. East Coast Akalat. BirdLife Species Fact Sheet. Available at www.birdlife.org. Accessed 30 January 2014.

Blanco, G. & Fargallo, J.A. (2013). Wing whiteness as an indicator of age, immunocompetence, and testis size in the Eurasian Black-Billed Magpie (*Pica pica*). *Auk*, **130**, 399-407.

Brook, B.W., O'Grady, J.J.,Chapman, A.P., Burgman, M.A., Akçakaya, H.R. & Frankham, R. (2000). Predictive accuracy of population viability analysis in conservation biology. *Nature* **404**, 385-387.

Caswell, H. (2001). Matrix Population Models: Construction, Analysis, and Interpretation, second ed. Sinauer, Sunderland, MA.

Clark, M.E. & Martin, T.E. (2007). Modeling tradeoffs in avian life history traits and consequences for population growth. *Ecol Model* **209**, 110-120.

Freeman, S.N., Noble, D.G., Newson, S.E. & Baillie, S.R. (2007). Modelling population changes using data from different surveys: the Common Birds Census and the Breeding Bird Survey. *Bird Study* **54**, 61-72.

Gilroy, J.R., Virzi T., Boulton, R.L. & Lockwood, J.L. (2012). Too few data and not enough time: approaches to detecting Allee effects in threatened species. *Conserv Lett* **5**, 313-322.

Gotelli, N. & Ellison, A. (2006). Forecasting extinction risk with nonstationary matrix models. *Ecol Appl* **16**, 51–61.

Hernández-Matías, A., Real, J.,Moleón, M., Palma, L., Sánchez-Zapata, J.A., Pradel, R. Carrete, M., Gil-Sánchez, J.M., Beja, P., Balbontín, J., Vincent-Martin, N., Ravayrol, A., Benítez, J.R., Arroyo, B., Fernández, C., Ferreiro, E. & García, J. (2013) From local monitoring to a broad-scale viability assessment: a case study for the Bonelli's Eagle in western Europe. *Ecol Monogr* **83**, 239-261.

Holmes, E.E. (2001). Estimating risks in declining populations with poor data. *Proc Nat Acad Sci* **98**, 5072-5077.

IUCN (International Union for the Conservation of Nature) 2012. Available at www.iucnredlist.org. Accessed 30 January 2014.

Karanth, K. U., Nichols, J. D., Seidenstricker, J., Dinerstein, E., Smith, J. L. D., McDougal, C., Johnsingh, A. J. T., Chundawat, R. S. & Thapar, V. (2003). Science deficiency in conservation practice: the monitoring of tiger populations in India. *Anim Conserv*, **6**, 141–146.

Kendall, W.L., Peterjohn, B.G. & Sauer, J.R. (1996). First-time observer effects in the North American Breeding Bird Survey. *Auk* **113**, 823-829.

Leslie, P.H. (1945). On the use of matrices in certain population dynamics. *Biometrika* **33**,184-212.

Link, W.A., Sauer, J.R. & Niven, D.K. (2006) A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. *Condor* **108**, 13-24.

Matiku, P.M., Bennun, L.A. & Nemeth, E. (2000). Distribution and population size of the threatened East Coast Akalat in Arabuko-Sokoke Forest, Kenya. *Ostrich* **71**, 282-285.

Morris, W.F. & Doak, D.F. (2002). Quantitative Conservation Biology: Theory and Practice of Population Viability Models. Sinauaer Associates, Inc., Sunderland, MA.

Newson, S.E., Woodburn, R.J.W., Noble, D.G., Baillie, S.R. & Gregory, R.D. (2005). Evaluating the Breeding Bird Survey for producing national population size and density estimates. *Bird Study* **52**, 42-54.

Rappole, J.H., McShea, W.J. & Vega-Rivera, J. (1993) Evaluation of two survey methods in upland avian breeding communities. *J Field Ornithol* **64**, 55-70.

Remsen, J.V. & Good, D.A. (1996). Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* **113**, 281-298.

Simberloff, D. (1988). The contribution of population and community biology to conservation science. Annu Rev Ecol Evol **19**, 473-511.

Stouffer, P.C., Johnson, E.I. & Bierregaard, R.O. Jr. (2013). Breeding seasonality in central Amazonian rainforest birds. *Auk*, **130**, 529-540.

Yearsley, J.M. (2004). Transient population dynamics and short-term sensitivity analysis of matrix population models. *Ecol Model* **177**, 245-258.

Observation Schedule (4 samples per year)	**Cost functional value**	**Parameter Estimates (F_3, G_1,G_2,P_3)**
One breeding sample	1.3804×10^{-9}	(2.0000, 0.3000, 0.8000, 0.9000)
Two breeding samples	1.9711×10^{-9}	(2.0000, 0.3000, 0.8000, 0.9000)
No breeding samples	1.0363×10^{-10}	(1.5286, 0.4942, 0.6354, 0.9000)

Table 1. Cost functional and life history parameter estimates values generated from inverse problems (ordinary least squares) using different sampling schemes.

FIGURE LEGENDS:

Figure 1. Simulated akalat population size for monthly samples over five years for (a) immature, (b) sub-adult, and (c) full adult akalats.

Figure 2. Simulated akalat population size for four monthly samples per year over five years including one breeding sample for (a) immature, (b) sub-adult, and (c) full adult akalats.

Figure 3. Simulated akalat population size for four monthly samples per year over five years including two breeding samples for (a) immature, (b) sub-adult, and (c) full adult akalats.

Figure 4. Simulated akalat population size for four monthly samples per year over five years including no breeding samples for (a) immature, (b) sub-adult, and (c) full adult akalats.

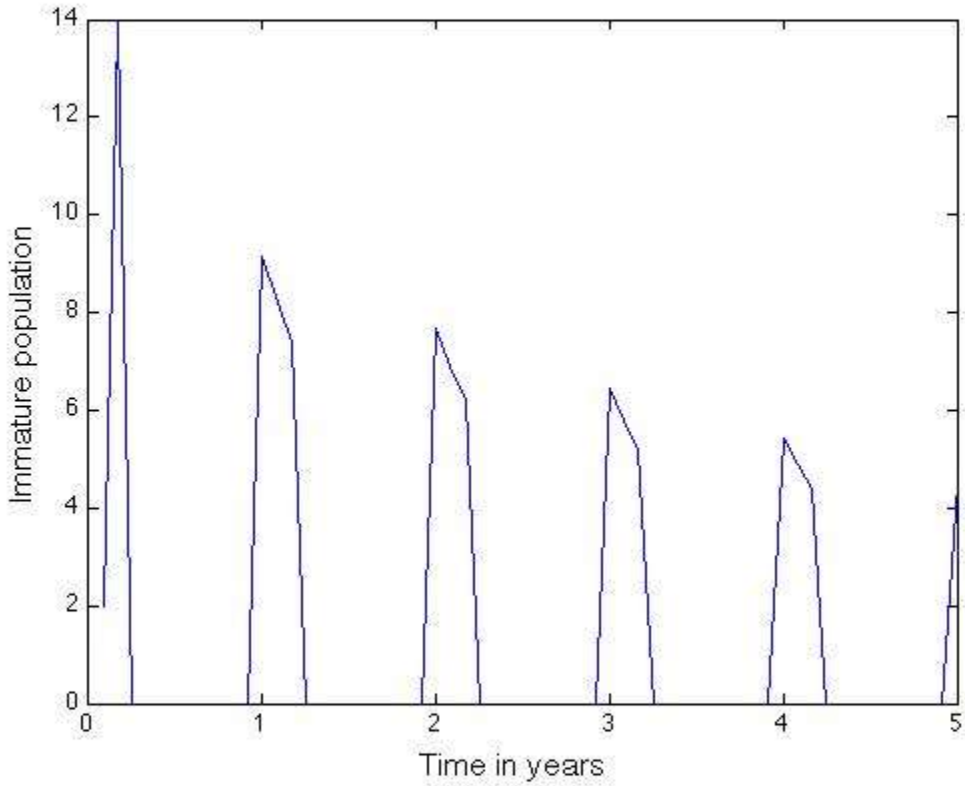

Figure 1(a): Monthly samples; immatures.

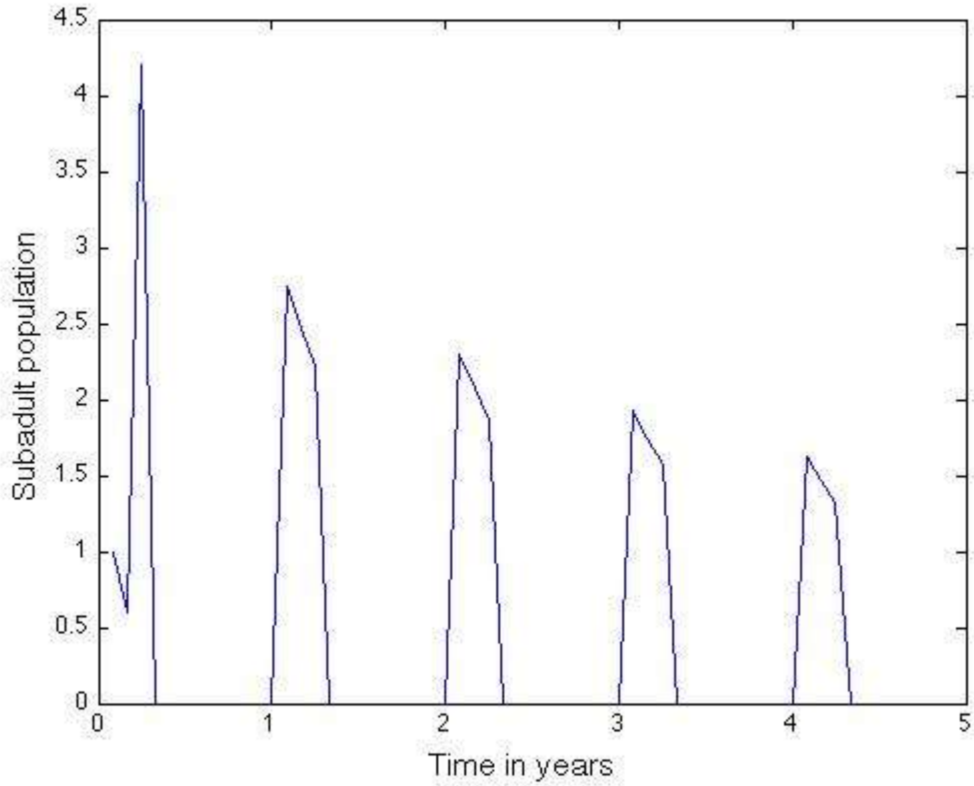

Figure 1(b): Monthly samples; sub-adults.

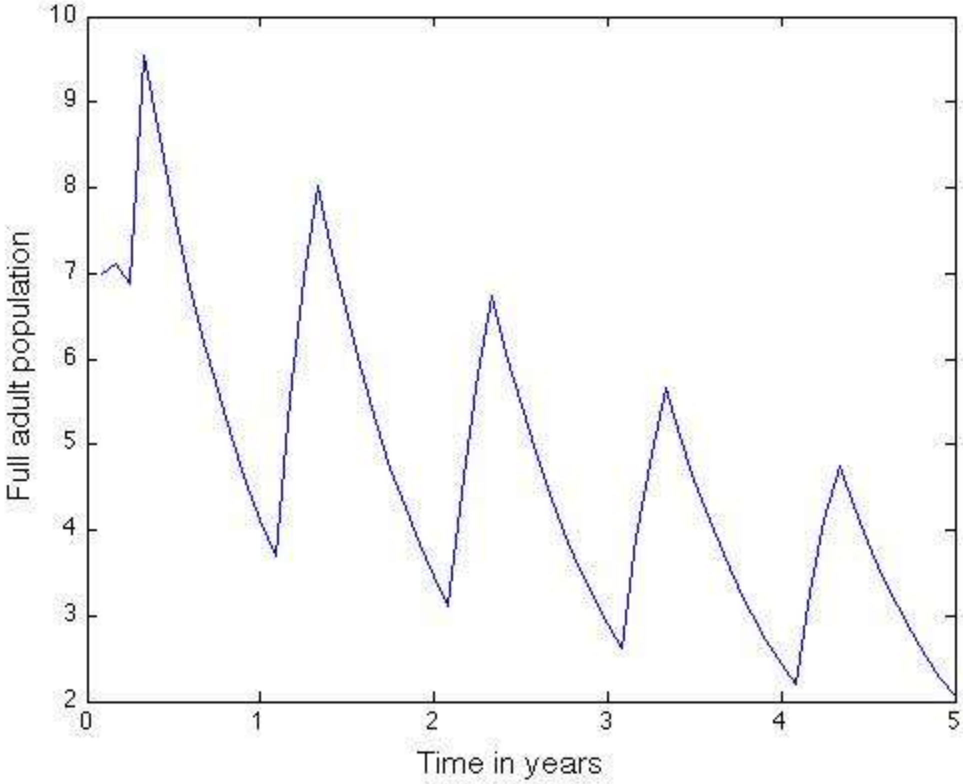

Figure 1(c): Monthly samples; full adults.

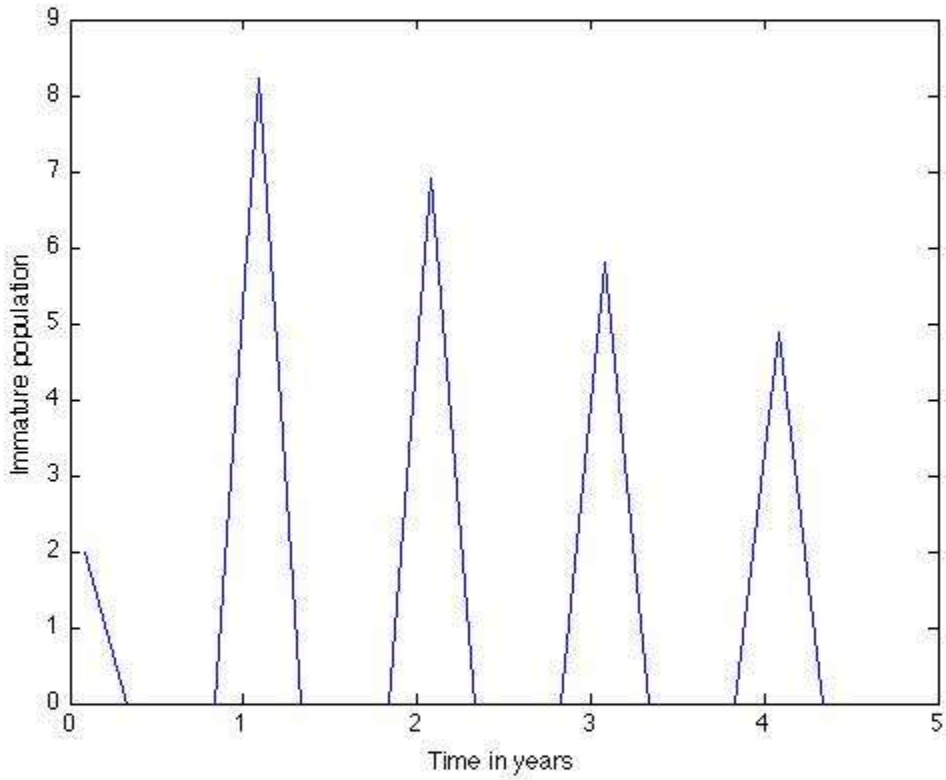

Figure 2(a): 4 samples per year (1 breeding sample); immatures.

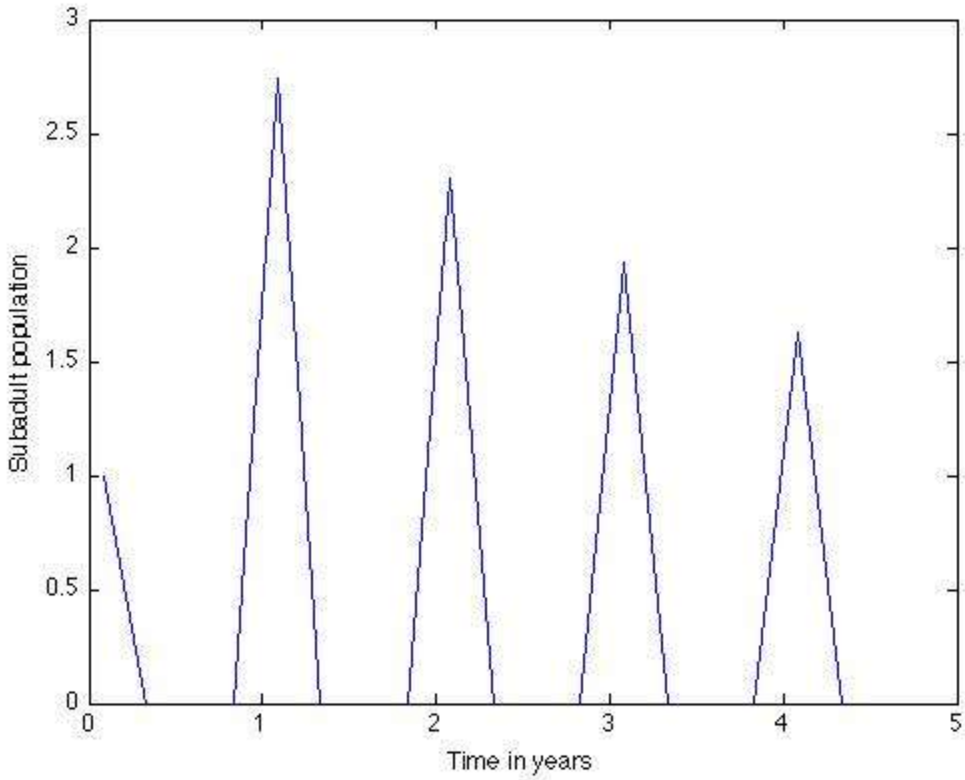

Figure 2(b): 4 samples per year (1 breeding sample); sub-adults.

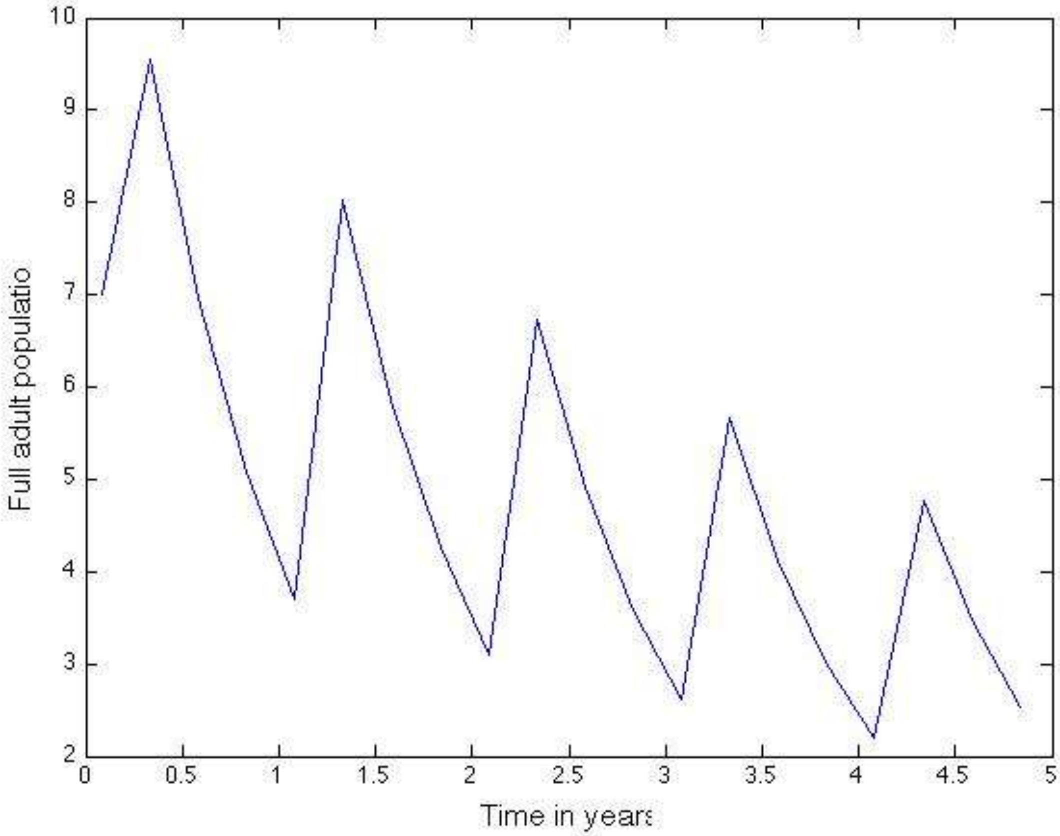

Figure 2(c): 4 samples per year (1 breeding sample); full adults.

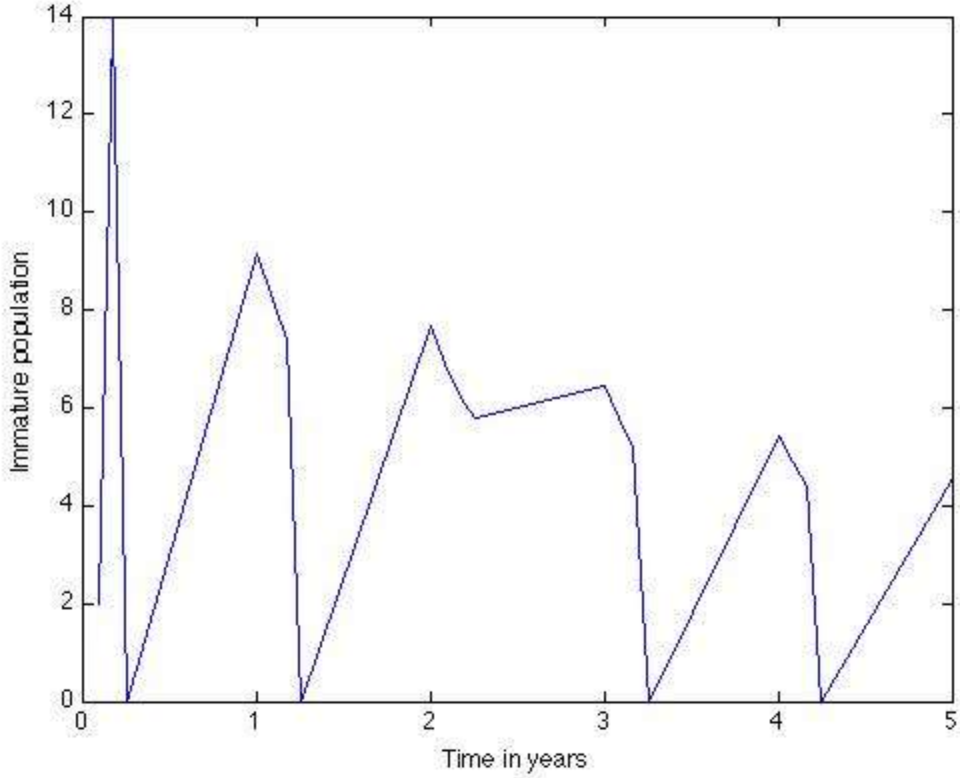

Figure 3(a): 4 samples per year (2 breeding samples); immatures.

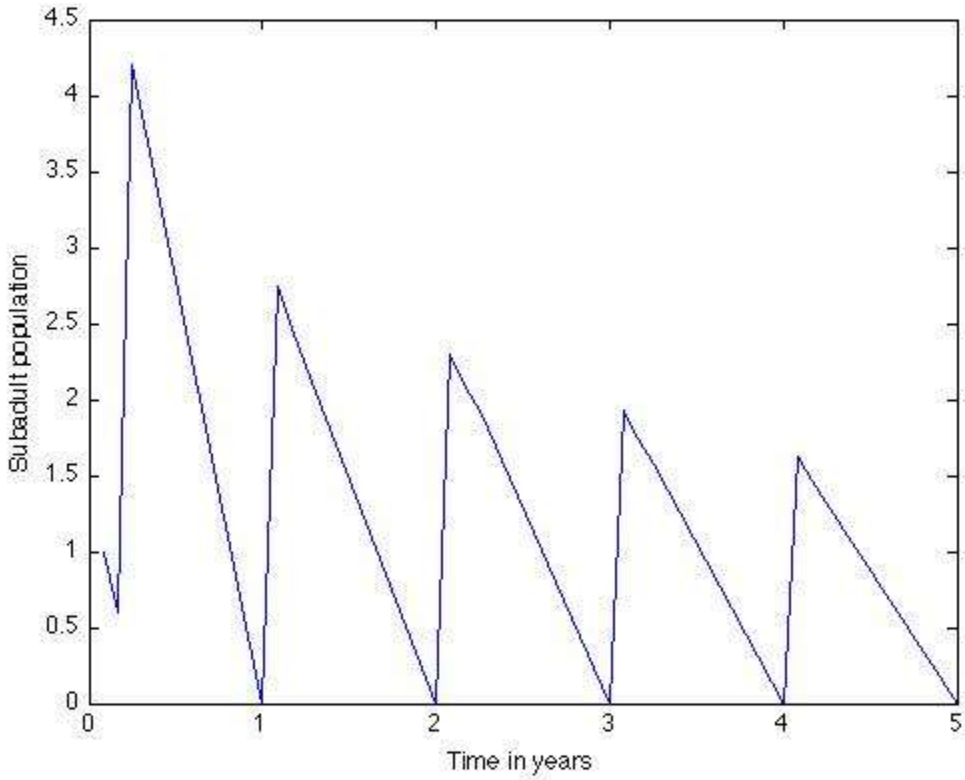

Figure 3(b): 4 samples per year (2 breeding samples); sub-adults.

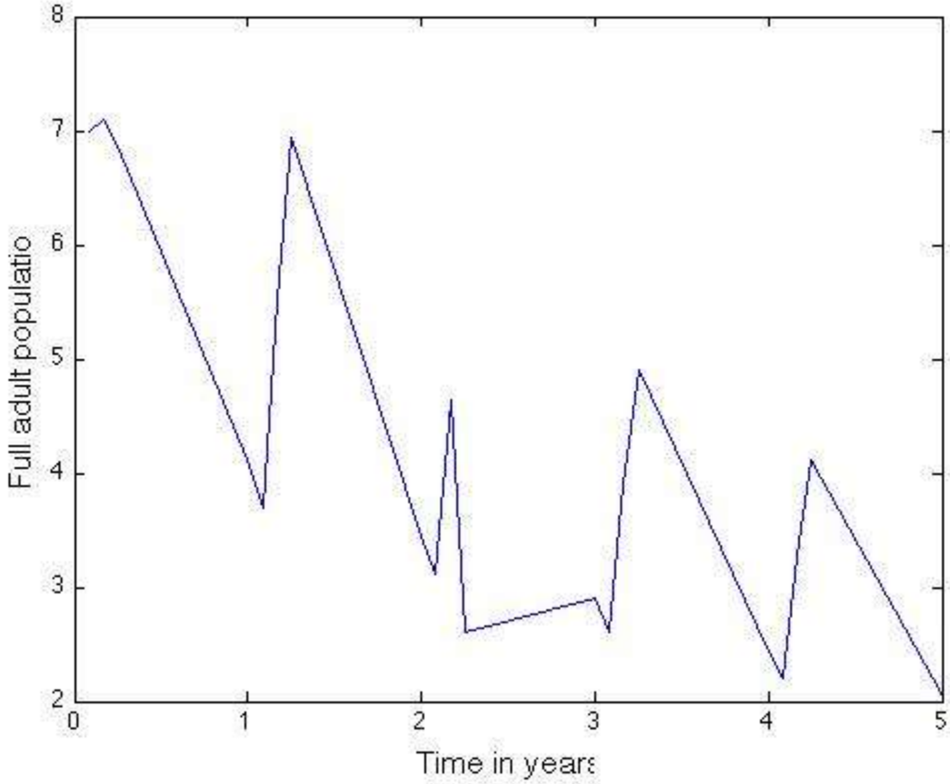

Figure 3(c): 4 samples per year (2 breeding samples); full adults.

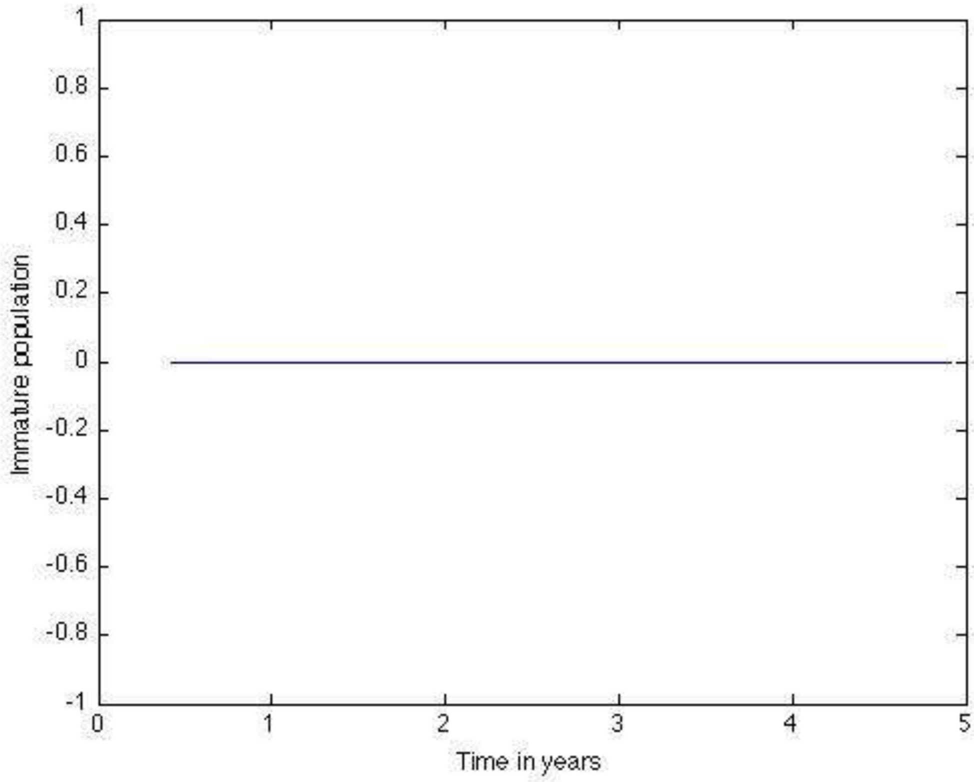

Figure 4(a): 4 samples per year (0 breeding samples); immatures.

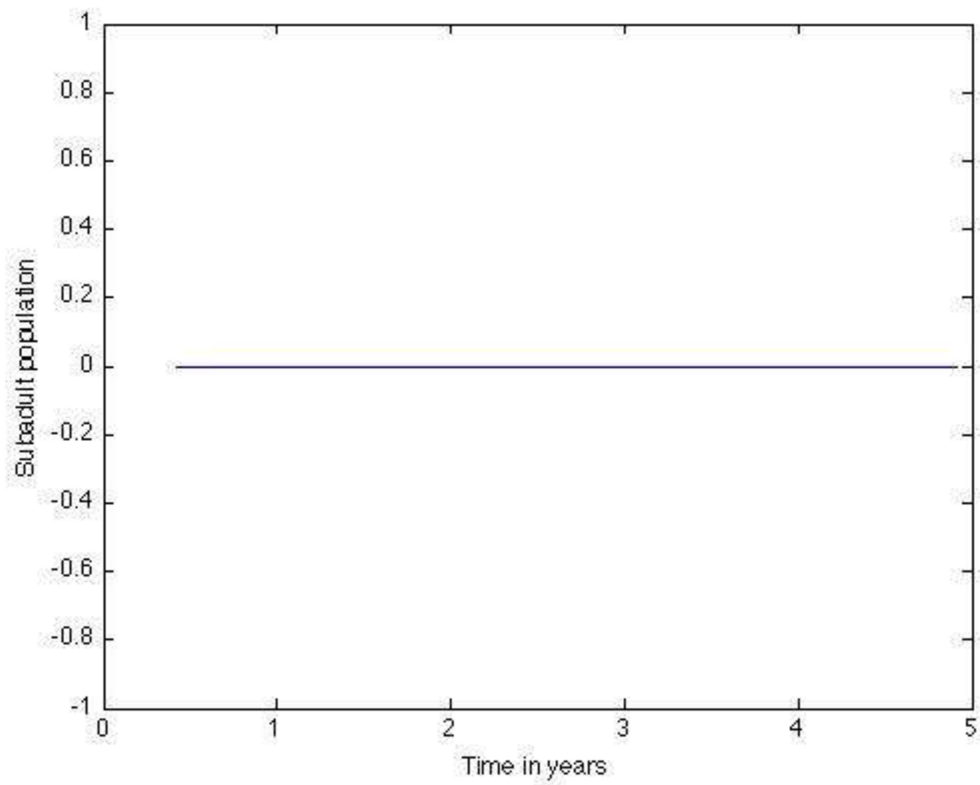

Figure 4(b): 4 samples per year (0 breeding samples); sub-adults.

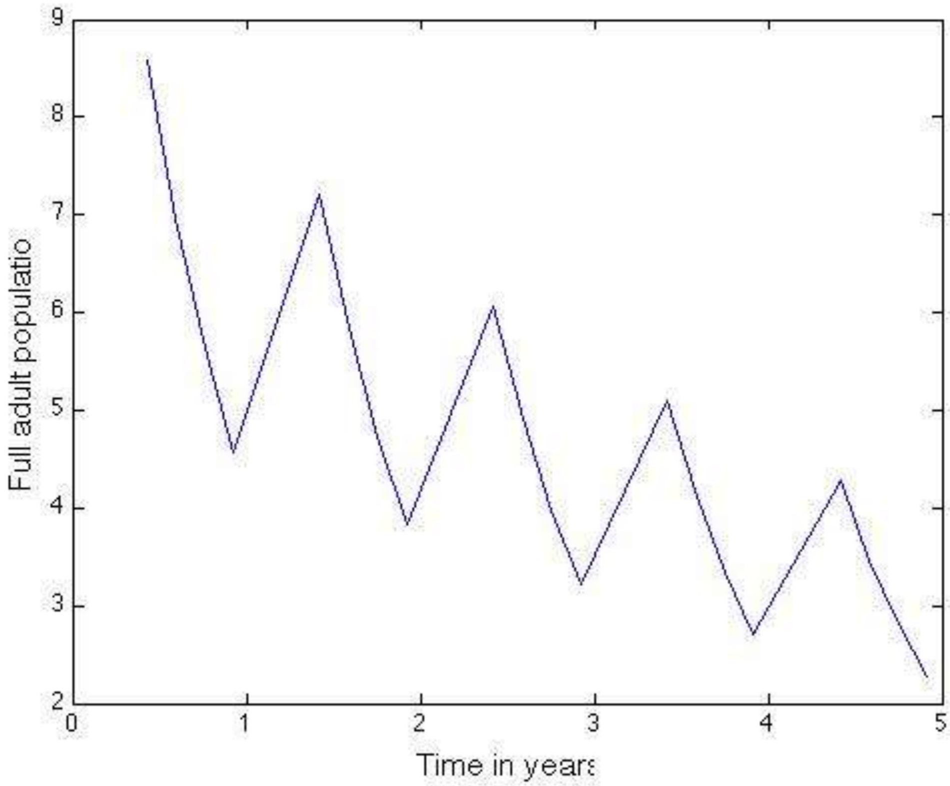

Figure 4(c): 4 samples per year (0 breeding samples); full adults.

APPENDIX I

Number of East Coast Akalats (*Sheppardia gunningi*) captured in mist nets in ringing sessions in Arabuko-Sokoke Forest from 1999 to 2012.

Session	**Immature**	**Subadult**	**Full Adult**	**Total**
Dec 1999	0	1	0	1
Feb 2000	2	0	0	2
Oct 2000	3	1	5	9
Nov 2000	1	0	1	2
June 2001	0	1	2	3
Aug 2001	0	0	6	6
Aug 2002	0	0	3	3
Sept 2002	0	1	1	2
May 2003	0	0	1	1
Feb 2005	0	1	4	5
Sept 2005	0	2	4	6
Oct 2007	0	0	1	1
Apr 2008	0	0	1	1
June 2008	0	0	2	2
July 2008	0	0	2	2
Aug 2008	0	6	3	9
Sept 2008	3	0	0	3
Oct 2008	1	0	2	3
Nov 2008	1	0	2	3
May 2009	0	1	3	4
Feb 2010	0	0	2	2
Sept 2010	1	0	1	2
Feb 2012	2	0	4	6
May 2012	1	0	2	3