Detection probabilities of ungulates in the eastern Swaziland lowveld

Bret A. Collier[1*], Robert A. McCleery[2], Kirby W. Calhoun[3], Kim G. Roques[4] & Ara Monadjem[5]

[1]*Institute of Renewable Natural Resources, Texas A&M University, College Station, Texas 77843, U.S.A.*
[2]*Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, U.S.A.*
[3]*Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843, U.S.A.*
[4]*All Out Africa, P.O. Box 153, Lobamba, Swaziland*
[5]*All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland*

Received 21 October 2010. Accepted 21 March 2011

The management of large ungulates in southern Africa necessitates reliable monitoring programmes to direct management action. Monitoring programmes for large ungulates typically rely on spotlight survey methods, but do not address variation in detection rates between surveys or observers. In 2009, we used a multiple observer survey technique to estimate detection probabilities for large ungulates in lowveld savanna habitats in Swaziland. Spotlight detection probabilities for all ungulates ranged between 0.22 and 0.57. Species-specific spotlight detection rates for the two most detected species, impala (*Aepyceros melampus*) and blue wildebeest (*Connochaetes taurinus*), were 0.48 and 0.61, respectively. At our open savanna study site, detection rates were higher and abundance estimates were fairly consistent. In our more enclosed savanna habitat, both detection rates and resulting abundance estimates were variable. Our results suggest that when monitoring large ungulate populations, managers should conservatively assume they are missing approximately 50% of the population available for surveying. We recommend that managers consider methods which incorporate multiple observers into survey practices and consider using multiple data sources to assist with population management decisions.

Key words: detection probability, double observer, ungulates, spotlight surveys.

INTRODUCTION

Efficient management of economically and socially important wildlife resources necessitates regular surveys to monitor population trends and develop appropriate management options. Thus, monitoring methods which are practical and efficient and provide accurate data are required for sound wildlife management (Morrison *et al.* 2008). In southern Africa, tourism can provide much needed revenue to rural communities (Samuelsson & Stage 2007), thus land managers make considerable efforts to manage charismatic ungulate species, often encouraging high densities. In the Swaziland lowveld, as with many areas in the region, savanna habitats on protected private and public lands represent oases of wildlife habitat. However, the small size and human-made barriers on protected lands (*e.g.* fencing) can restrict natural wildlife movement patterns and lead to fire suppression or atypical burn cycles affecting plant distribution, density, and richness. Coupled with the frequent inability to accommodate sustainable populations of large predators (Power 2003; Lindsey *et al.* 2004), management activities on smaller properties often lead to unchecked growth in ungulate populations (Skogland 1991). Elevated populations of ungulates can disrupt succession of native vegetation, cause fire suppression, both which reduces the general health and quality of the savanna community (Scholes & Walker 1993). To deal with these potential issues, wildlife managers often harvest ungulates as a management strategy to keep populations in equilibrium. However, for population management to be successful, accurate population assessment is necessary.

One of the most common methods used to assess population size and trend of ungulates is spotlight counts (Gaidet-Draper *et al.* 2006; Collier *et al.* 2007). Vehicle-based spotlight counts allow managers to cover a large area, and are inexpensive and logistically simple compared to techniques such as camera trapping or aerial surveys. Furthermore, the risks associated with spotlighting are minimal compared with other survey methods (*e.g.*

*To whom correspondence should be addressed.
E-mail: bret@tamu.edu

flight dangers; Pollock & Kendall 1987). Spotlight surveys are widely used for monitoring population trends of ungulates (Fafarman & DeYoung 1986; Garton *et al.* 2005). Although biases associated with using spotlight surveys are well documented (Collier *et al.* 2007), spotlight surveys are still actively used in wildlife management and monitoring. Typically, estimates based on spotlight surveys are negatively biased due to imperfect detection of individuals (Williams *et al.* 2001); although several authors have suggested that relative indices of abundance can be used for management purposes by tracking population trends over time (Winchcombe & Ostfeld 2001; Johnson 2008). However, the broad array of factors which can affect detection rates (*e.g.* observer differences, habitat conditions, transect location) make it difficult, if not impossible, to garner accurate estimates of population size or trend from spotlight surveys as currently used (Collier *et al.* 2007).

Development and application of surveying methods which adjust for variability in detection probability due to observer or methodological differences has been a fruitful area of wildlife research (see Williams *et al.* 2001 for a review). However, many biologists and land managers lack experience or interest in the statistical theory and application underlying quantitative methods often used (*e.g.* Distance sampling; Buckland *et al.* 2001; Stenkewitz *et al.* 2010). Thus, we expect spotlight surveys to remain a widely used method for monitoring ungulate abundance in southern Africa as spotlights require less intensive data collection and analysis methods than those typically associated with survey sampling. Nonetheless, methods using multiple observers provide one potential opportunity to simply correct for bias during population surveys which is the primary issue hindering wildlife population estimation (Williams *et al.* 2002). Thus, where opportunities exist, we feel it is important to conduct observational studies which provide estimates of variability in species detectability which can be used with future survey data for outlining management actions to address observational variability in wildlife surveys. Here, we outline a study focused on determining detection rates of ungulates in an African savanna system. The goals of our study were to estimate observer-specific variation in detection probabilities during ungulate surveys using standard spotlight survey methods compared to thermal imaging methods, and evaluate the validity of multiple observer survey methods as an alternative to spotlight surveys of ungulate populations on private lands in southern Africa.

STUDY AREA

Our research was conducted in the lowveld region of northeastern Swaziland near the Swaziland/Mozambique border. We conducted surveys at two locations, the Mlawula Nature Reserve (hereafter Mlawula) and the Mbuluzi Game Reserve (hereafter Mbuluzi). Both Mlawula and Mbuluzi form part of the greater Lubombo Conservancy region of eastern Swaziland and are nested within the larger Lubombo Transfrontier Conservation Area (Anonymous 1992). Mlawula is a ~16 500 ha lowveld bushveld region with vegetative communities dominated by acacias (*Acacia spp.*) ironwood (*Combretum imbere*) and marula (*Sclerocarya birrea*). The Mlawula River bisects Mlawula in the north with small tributaries feeding into the river from throughout the reserve. Mbuluzi supports ~2500 ha of sour bushveld of the same woody vegetative communities as Mlawula; however, management using brush clearing, prescribed fire and managed grazing has allowed for a more open grassland savanna while Mlawula consisted of a more dense vegetative community with less grassland savanna.

METHODS

We conducted surveys between 8 and 12 January 2009 (8th and 10th in Mlawula, 9th and 12th in Mbuluzi) using standard protocols for road-based spotlight surveys (Mitchell 1986). Observers were located in the rear of a pickup truck travelling approximately 10 km/h, with a thermal imager surveyor at the front of the truck bed and the spotlight observer located at the rear of the truck bed. Both surveyors would sweep back and forth perpendicular to the vehicle searching for ungulates. Observers were separated and instructed not to discuss observations such that the other surveyor would not be able to cue on any missed individuals based on actions of the other surveyor. In order to evaluate accuracy of spotlights relative to an alternative method we followed the approach and methods used by Collier *et al.* (2007) wherein we used a double observer approach with two different detection methods (thermal imager, spotlight). For each survey, two observers, one with the thermal imager, one with the spotlight, surveyed one side of the vehicle and independently collected data on ungulates identified using each survey method. We designated the thermal imager to be the first (capture) observer and treated spotlight surveyors to be the recapture observer. We used the thermal imager as the standard to test the efficacy of observers using spotlights for ungulate surveys (Collier *et al.* 2007). During surveys, when the spotlight surveyor located individuals, we stopped the vehicle to ensure the spotlight observer was able to accurately ascertain species number and composition. At this time, the thermal imaging observer would relay the time stamp for those observations to ensure that each observation noted by the spotlight was accurately recorded. We did not stop the vehicle for thermal imaging observations as that would have artificially cued the spotlight observer in on those individuals. While we followed the methods and protocol of Collier *et al.* (2007), we note that under a multiple observer method that two observers with spotlights would also be an appropriate method for estimating detection rates.

We used a Raytheon Palm IR (FLIR ThermaCAM® B-20 FLIR Systems, North Billerica, Massachusetts, U.S.A.) located at the front of the vehicle while spotlight observers were located at the rear of the vehicle and used Lightforce SL 240 spotlights (Lightforce U.S.A., Inc., Orofino, Idaho, U.S.A.). To reduce misclassification bias associated with identified individuals or groups (Williams *et al.* 2002); we uniquely identified each observation using a unique time-specific identifier and checked those times during each event where the spotlight located a individual to ensure that times of spotlight detection were identified correctly by the thermal imager. We assumed that 1) capture events were independent, 2) detection by one method did not cue in the other observer to individuals and we followed all other protocols detailed in Collier *et al.* (2007). We conducted our surveys on the standard survey routes used by field biologist staff on Mlawula and Mbuluzi with surveys beginning shortly after dusk and lasting between three and four hours (distance ranging between 10 and 16 km). We used the same survey routes during both surveys at each site.

Data analysis

We considered each individual to be unique whether captured individually or as part of a group (Collier *et al.* 2007) and while we distinguished between species when possible during our surveys, we only address species-specific detection rates where we had adequate encounters to develop an encounter history. We used a two-sample Huggins closed capture model (Huggins 1989; 1991) implemented in program MARK (White and Burnham 1999) using RMark (Laake & Rexstad 2009). Following Collier *et al.* (2007), we let i = detection with the thermal imager and j = detection with the spotlight and we define i and j = 1 when an individual was captured (*e.g.* seen by thermal imager or spotlight) and = 0 when an individual was not captured (*e.g.* not seen by the thermal imager or spotlight). We considered capture occasions temporally, wherein the initial capture represents those individuals captured by the thermal imager and the second capture represents individuals captured by the spotlight, giving us three unique capture histories (11, 10, 01) for each of k observer pairs.

We considered a candidate model set of six a priori models which address hypotheses on differences between methods, observers, and survey sites. Our model set ranged from no differences between the above (no. parameters = 1) to one for which we expected differences between methods, observers, and transects (no. parameters = 8; Table 1). We evaluated model fit relative to the data and other potential models using a small sample size adjusted AICc (Burnham & Anderson 2002) in MARK (White & Burnham 1999). Following Collier *et al.* (2007), we estimated detection probability for each observer and method, as well as deriving estimates of site level abundance and associated confidence intervals. For species-specific detection estimation, we used a single model where detection rates differed between thermal imager surveyors and spotlight surveyors, holding effects of transect constant as we had to few observations within each transect to allow for transect level estimation.

RESULTS

We identified 245 unique individuals during the surveys (Table 2). Spotlight surveyors detected a wide variety of ungulates in varying frequencies, including; impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus),* common duiker (*Sylvicapra grimmmia*), nyala (*Tragelaphus angasii*), waterbuck (*Kobus ellipsiprymnus*), giraffe (*Giraffa camelopardalis*), zebra (*Equus quagga*), and bushbuck (*Tragelaphus scriptus*). The thermal imager (TI) alone detected 78% of the total ungulates seen whereas the spotlight (SL) detected 55%. Based on our detection data, we detected a wider variety of species at Mbuluzi (nine; all species

Table 1. Candidate model set and model selection criteria used to evaluate detection probabilities of ungulates during double observer thermal imager and spotlight surveys in Mlawula Nature Reserve and Mbuluzi Game Reserve in Swaziland during 2009.

Model	–2 log likelihood	ΔAICc	Number of parameters	w_i	Deviance
Model 1[a]	436.628	0	8	1.0	1594.74
Model 2[b]	474.147	33.393	6	0	1632.26
Model 3[c]	473.936	35.241	7	0	1632.05
Model 4[d]	495.894	53.091	5	0	1654.01
Model 5[e]	517.957	69.054	2	0	1676.07
Null Model[f]	538.317	87.398	1	0	1696.42

[a]Capture and recapture probabilities different between both observers and survey.
[b]Capture probability constant between surveys but differs by site, recapture probability different between observers.
[c]Capture probability differs by observer and site, recapture probability differs by observer.
[d]Capture probability constant, recapture probability differs by survey.
[e]Capture and recapture probability different but constant between surveys.
[f]Capture and recapture probability constant and equal between surveys and observers.

listed above) than at Mlawula (three; only greater kudu, impala, wildebeest). The most frequent species observed over both survey periods in Mlawula was wildebeest (53% of observations) while impala were the most frequently detected ungulate in Mbuluzi (23% of observations). We had limited observations at either location of bushbuck (2), common duiker (3), and waterbuck (1) during the four surveys.

Using the data collected during our surveys, the most parsimonious model was one where ungulate detection rates varied between the thermal image capture observer and the spotlight capture observer, between each survey transect, and for each survey (Table 1). This model was by far the best given the data, as the ΔAIC_c value between this model and the next best fitting model was 33.39 units (Table 1). The best fitting model indicated that detection rates were typically higher using the thermal imager (Fig. 1), except during Mlawula survey 1 where few observations were made by the thermal imager relative to the spotlight (Table 2). Detection rates with the thermal imager varied for each survey occasion (0.13 (S.E. = 0.05), 0.78 (S.E. = 0.07), 0.75 (S.E. = 0.22, 0.84 (S.E. = 0.05)) were usually higher than spotlight survey detection estimates (0.22 (S.E. = 0.08), 0.42 (S.E. = 0.06), 0.13 (S.E. = 0.07), 0.57 (S.E. = 0.06)) although note that spotlight detection rates were higher during the initial survey in Mlawula, likely due to our learning the intricacies of thermal-imager unit used during that survey. Counts using spotlights were usually lower than counts using the thermal imager (Table 2) and detection corrected estimates of abundance show the impact of under-estimating detection rates on the number of ungulates along survey transects (Fig. 1). We were able to estimate species-specific detection probabilities for two species, impala and blue wildebeest. Detection probabilities for blue wildebeest were lower with the thermal imager (0.242 (S.E. = 0.20)) than with the spotlight (0.61 (S.E. = 0.085)), while detections for impala showed the opposite results, being higher using the thermal

Table 2. Numbers of unique ungulates detected and encounter history for each management area by survey transect designation and survey replicate (1, 2). The first number in the encounter history refers to detection (1) or non-detection (0) by the capture observer (thermal imager) while the second numeral refers to detection (1) or non-detection (0) by the recapture observer (spotlight) during simultaneous observations in Mlawula Nature Reserve and Mbuluzi Game Reserve in Swaziland during 2009.

	Mlawula		Mbuluzi	
Encounter history	Survey 1	Survey 2	Survey 1	Survey 2
11	5	31	3	43
10	17	42	19	32
01	35	9	1	8
Total	57	82	23	83

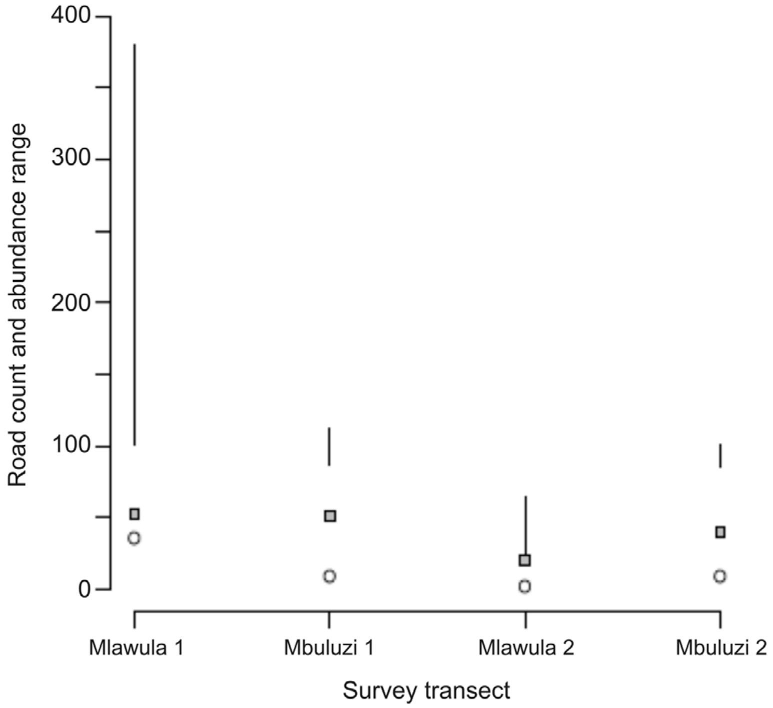

Fig. 1. Counts of ungulates seen by each observer pair for two replicated survey transects (Mlawula and Mbuluzi) in Swaziland during January 2009. Spotlight counts are shown as circles, total of both spotlight and thermal imagers are shown as squares and the 95% confidence intervals for the derived abundance estimates from a Huggins double observer closed capture model are shown as line segments.

imager (0.77 (S.E. = 0.086)) than with the spotlight (0.49 (S.E. = 0.080)).

DISCUSSION

Accurate estimation of population size has been one of the primary foci for wildlife managers across the world. In general, our results indicate that observers conducting spotlight surveys would detect approximately half of those individuals which were available for detection. There was considerable variation in estimated abundance at Mlawula, likely due to lower detections using the thermal imager during the initial survey period. Note that estimates for Mbuluzi were consistent for the two survey periods, suggesting that the high amount of variation in the first Mlawula survey was likely an artefact of observer variation associated with initial application of the thermal imager to ungulate surveys. However, detection rates for spotlight observers varied significantly between observers and survey sample occasions, ranging from 0.13 to 0.57, agreeing with previous work on spotlight surveys indicating that individuals are missed variably during surveys (Forcardi *et al.* 2001; Drake *et al.* 2005; Potvin & Breton 2005). For our estimates of species-specific detections, blue wildebeests were more likely to be detected using the spotlight than using the thermal imager. We suspect that this occurred for two reasons; 1) blue wildebeest, when found, tended to exist in groups and were thus less uniquely identifiable using the thermal imagers, and 2) because spotlight surveyors were able to obtain better image quality using binoculars and the spotlights than those the thermal imager surveyors were able to (*e.g.* Collier *et al.* 2007). Detections of impala were much higher with the thermal imager than the spotlight, with the spotlight detecting on average 48% of those individuals available during the survey, in rough concordance with double observer survey estimates (Collier *et al.* 2007).

Most work with spotlight surveys has typically focused on single species surveys such as white-tailed deer (*Odocoileus virginianus*) (see Mitchell 1986; Collier *et al.* 2007 and references therein); however, as there are a wide variety of ungulate species in Africa, we expect detection functions to be potentially different dependent on factors such as size, survey season, species gregariousness, or relationships with habitat types (Stenkewitz *et al.* 2010). We had so few detections of some species (*e.g.* 12 greater kudu detections, ≤6 duiker, ≤10 nyala) that accurate estimation of detection probabilities for each method across survey sites, transects, or between unique observers would be difficult in our study. However, with increased replication, one could perhaps identify general trends in detection probabilities for each species.

We made no assumptions regarding the underlying sampling frame used for spotlight surveys in Swaziland. Obviously, our use of road-based survey transects will provide at best a biased estimate of ungulate population size, dependent on the distribution of ungulates relative to the surveyed roads (Buckland *et al.* 2001; Collier *et al.* 2007; Johnson 2008). However, spotlight surveys are commonly used to monitor many ungulate populations worldwide because of their economic value and ease of use (Garton *et al.* 2005). Our results agree with those results found by Collier *et al.* (2007) indicating that a generality likely exists regarding underestimation when spotlights surveys are used to monitor ungulate populations. In addition, we found that factors causing variation in detection probabilities for ungulates was consistent with those results found by Collier *et al.* (2007). Thus, when conducting spotlight surveys, biologist should expect considerable difference in detection rates among observers and surveys. Thus, we recommend that managers use the same individuals for all spotlight counts for consistency in rates of detection. Furthermore, we consider it important for managers to realize that spotlight counts, even with consistent detection rates, are indices and best used for determining population trends (Winchcombe & Ostfeld 2001; Johnson 2008). We would caution managers from translating spotlight counts into population estimates for stocking rates or other purposes but if they do we would suggest doubling their estimated abundance for very coarse and conservative estimates . We believe a better approach would be to use spotlight data in conjunction with other monitoring methods such as vegetation monitoring, camera surveys, or a variety of other methods (Kraaij & Milton 2006; Ditchkoff 2007; McCoy *et al.* 2011) focused on conditions of the grassland savanna. Additionally, although perhaps cost prohibitive, use of thermal imagers seems to provide a less biased estimate of detection probabilities for ungulates, thus managers could potentially consider thermal imaging for surveying ungulates in African savanna.

In conclusion, although spotlight surveys are frequently applied due to convenience and cost, they likely provide only an index of population size or trend. A variety of methods are available that could supersede use of traditional summary methods using spotlight surveys for those individuals interested in increasing their knowledge of population estimation methods. We do not recommend against spotlight use for surveying per se; however, we suggest that the application of different estimation techniques using appropriately collected data would provide a much more accurate estimate of population trends than standard summary count data. For example, we suggest that although standard distance sampling (Thomas *et al.* 2010) methods are applicable to abundance estimation, following Collier *et al.* (2007) we recommend that updated mark–recapture distance sampling techniques applicable to line-transect sampling (Borchers *et al.* 2006; Laake *et al.* 2008) represent an underused, but highly applicable method for addressing issues associated with imperfect detection on the transect line (*e.g.* assumption that g(0) = 1; Laake & Borchers 2004) combined with the effects of distance on detection probabilities.

ACKNOWLEDGEMENTS

This is the 18th communication of the All Out Africa Research Unit (www.alloutafrica.org). We are grateful to All Out Africa for logistic support in the field. We thank Ngwane Dlamini, Senior Warden of Mlawula Nature Reserve for permitting our work at Mlawula, as well as Matt McGinn, Manager of Mbuluzi Game Reserve, for our work at Mbuluzi. We are grateful to the students in the African Wildlife Ecology class from Texas A&M University for their assistance with field work. Support for this project was provided by the Texas A&M University Study Abroad Office and the Texas A&M Institute of Renewable Natural Resources.

REFERENCES

ANON. 1992. Lumbombo transfrontier conservation and resource area protocol. Government of Swaziland, Mbabane.

BUCKLAND, S.T., ANDERSON, D.R., BURNHAM, K.P., LAAKE, J.L., BORCHERS, D.L. & THOMAS, L. 2001. Introduction to distance sampling. Oxford University Press, Oxford.

BORCHERS, D.L., LAAKE, J.L., SOUTHWELL, C. & PAXTON, C.G.M. 2006. Accommodating unmodeled heterogeneity in double-observer distance sampling surveys. *Biometrics* 62: 372–378.

BURNHAM, K.P. & ANDERSON, D.R. 2002. Model selection and multimodel inference. Springer-Verlag. New York.
COLLIER, B.A., DITCHKOFF, S.S., RAGLIN, J.B & SMITH, J.M. 2007. Detection probability and sources of variation in white-tailed deer spotlight surveys. *J. Wildl. Manage.* 71: 277–281.
DRAKE, D., AQUILA, C. & HUNTINGTON, G. 2005. Counting a suburban deer population using forward-looking infrared radar and road counts. *Wildl. Soc. Bull.* 14: 180–185.
DITCHKOFF, S.S. 2007. Scientific vs. artistic deer management. *Wildl. Trends* 7: 7–11.
FAFARMAN, K.R. & DEYOUNG, C.A. 1986. Evaluation of spotlight counts of deer in South Texas. *Wildl. Soc. Bull.* 14: 180–185.
FOCARDI, S, DE MARINIS, A.M., RIZZOTTO, M. & PUCCI, A. 2001. Comparative evaluation of thermal infrared imaging and spotlighting to survey wildlife. *Wildl. Soc. Bull.* 29: 133–139.
GAIDET-DRAPIER, N., FRITZ, H., BOURGAREL, M., RENAUD, P-C., POILECOT, P., CHARDONNET, P., COID, C., POULET, D. & LE BEL, S. 2006. Cost and efficiency of large mammal census techniques: a comparison of methods for a participatory approach in a communal area, Zimbabwe. *Biodiv. Conserv.* 15: 735–754.
GARTON, E.O., RATTI, J.T. & GIUDICE, J.H. 2005. Research and experimental design. In: C.Braun (Ed.), Techniques for wildlife investigations and management (6th edn) (pp. 43–71). The Wildlife Society, Bethesda.
HUGGINS, R.M. 1989. On statistical analysis of capture experiments. *Biometrika* 76: 133–140.
HUGGINS, R.M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47: 725–732.
JOHNSON, D.H. 2008. In defence of indices: the case of bird surveys. *J. Wildlife Manage.* 72: 857–868.
KRAAIJ, T. & MILTON, S.J. 2006. Vegetation changes (1995–2004) in semi-arid Karoo shrubland, South Africa: effects of rainfall, wild herbivores and change in land use. *J. Arid Environ.* 64: 174–192.
LAAKE, J.L. & BORCHERS, D.L. 2004. Methods for incomplete detection at distance zero. In: S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas (Eds), Advanced distance sampling (pp. 108–189). Oxford University Press, New York.
LAAKE, J.L. & REXSTAD, E. 2009. RMark: R code for MARK Analysis. R Package Version 1.9.5.
LAAKE, J.L., DAWSON, M. & HONE, J. 2008. Visibility bias in aerial survey: mark–recapture, line-transect, or both. *Wildl. Res.* 35: 299–309.
LINDSEY, P.A., DU TOIT, J.T. & MILLS, M.G.L. 2004. Area and prey requirements of African wild dogs under varying habitat conditions: implications for reintroductions. *S. Afr. J. Wildl. Res.* 34: 77–86.
McCOY, J.C., DITCHKOFF, S. S. & STEURY, T.D. 2011. Bias associated with baited camera sites for assessing population characteristics of white-tailed deer. *J. Wildlife. Manage* 75: 472–477.
MITCHELL, W.A. 1986. Deer spotlight census: section 6.4.3, U.S. Army Corp of Engineers wildlife resources management manual. U.S. Army Engineer Waterways Experiment Station Technical Report EL-86-53, Vicksburg.
MORRISON, M.L., BLOCK, W.M., STRICKLAND, M.D., COLLIER, B.A. & PETERSON, M.J. 2008. Wildlife study design. Springer-Verlag, New York.
POLLCOK, K.H. & KENDALL, W.L. 1987. Visibility bias in aerial surveys: a review of estimation procedures. *J. Wildlife Manage.* 51: 502–510.
POTVIN, F. & BRETON, L. 2005. From the field: testing 2 aerial survey techniques on deer in fenced enclosures – visual double counts and thermal infrared sensing. *Wildl. Soc. Bull.* 33: 317–325.
POWER, R.J. 2003. Evaluating how many lions a small reserve can sustain. *S. Afr. J. Wildl. Res.* 33: 3–11.
SAMUELSSON, E. & STAGE, J. 2007. The size and distribution of the economic impacts of Namibian hunting tourism. *S. Afr. J. Wildl. Res.* 37: 41–52.
SCHOLES, R.J. & WALKER, B.H. 1993. An African savanna. Synthesis of the Nylsvley study. Cambridge University Press, Cambridge.
SKOGLAND, T. 1991. What are the effects of predators on large ungulate populations. *Oikos.* 61: 401–411.
STENKEWITZ, U., HERRMANN, E. & KAMLER J.F. 2010. Distance sampling for estimating springhare, Cape hare, and steenbok densities in South Africa. *S. Afr. J. Wildl. Res.* 40: 87–92.
THOMAS, L., BUCKLAND, S.T., REXSTAD, E.A., LAAKE, J.L., STRINDBERG, S., HEDLEY, S.L., BISHOP, J.R.B., MARQUES, T.A. & BURNHAM, K.P. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47: 5–14.
WILLIAMS, B.K., NICHOLS, J.D. & CONROY, M.J. 2002. Analysis and management of animal populations. Academic Press, San Diego.
WINCHCOMBE, R.J. & OSTFELD, R.S. 2001. Indexing deer numbers with spotlighting: a long-term study of a managed deer population. *Northeast Wildl.* 56: 31–38.
WHITE, G.C. & BURNHAM, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement): 120–139.

Corresponding Editor: E.Z. Cameron