

**Chemical immobilization of African buffalo (*Syncerus caffer*)
in Kruger National Park: Evaluating effects on
survival and reproduction**

BY

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Note on the text

The text is formatted in the style of Journal of Wildlife Management to which it will shortly be submitted; therefore the tables and figures are presented at the end of the text in accordance to submission style.

ABSTRACT

We evaluate relationships between chemical immobilization, delayed mortality and calving rates of African buffalo *Syncerus caffer* in the Kruger National Park, South Africa. Although buffalo capture protocols are well researched, capture-related mortality and reduced calving rates may not be immediate and will be underestimated if animals are not monitored after capture. We used generalized linear models to model the survival response of repeatedly captured radiocollared buffalo, and the calving rates of cows between 2001 and 2005 as a function of different explanatory variables. Model selection was based on small sample Akaike Information Criterion (AICc). Evidence for capture effects is strong for both survival and calving rates, as models with a capture variable rank higher than those without the variable. Mortality is positively associated with captured individuals, but, capture effects are small relative to the influences of rainfall, sex and age, and they only reduce seasonal survival by 0-3%. Captures do not decrease the calving rate; rather captured cows show higher calving rates. Cows captured in late gestation show the highest reproductive success of 70-80%. The decrease in survival rate of captured buffalo caution that some capture-related delayed mortality may occur. However, capture-related mortality may be overestimated and model uncertainty predicts capture effects to be negligible at the buffalo population level. A slight negative observational bias exists for known females never captured due to greater observational challenges. Captures during late gestation may be biased to pregnant cows, artificially increasing the recorded calving rate. Still, cows do not abort when captured in late gestation. Biases in capture probability are unlikely to influence conclusions of other studies, but increase direct capture death risk. The captured sample is deemed to be representative of the population.

Keywords: African buffalo, AIC, chemical capture, reproduction, *Syncerus caffer*, survival

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Chemical immobilization of African buffalo (*Syncerus caffer*) in Kruger National Park: Evaluating effects on survival and reproduction

INTRODUCTION

An important assumption of observational and experimental studies is that the studied sample behaves in a natural way that is representative of the entire study population (White & Garrott 1990). Studied individuals should therefore be a sub-sample of the population, reflecting population characteristics (Tuytens *et al.* 2002). However, relatively few studies investigate the effect of immobilization and capture on mammals, even though these methods may adversely affect study populations or produce erroneous research results (Woolnough *et al.* 1998; Moorhouse & MacDonald 2005). This is possibly due to the inherent constraints associated with investigation of capture effects. Negative effects, even if important are likely to be subtle and difficult to detect (Tuytens *et al.* 2002). Capture effects can only be determined by thorough monitoring of captured and control individuals (Berger & Kock 1988). Unbiased control data of a cohort of animals that has not been handled in any way is difficult to obtain, and statistical analysis of data is often hampered by small sample sizes and experimental limitations (Laurenson & Caro 1994). It is therefore possible that detrimental effects go unobserved because they are rare, or simply not considered (Laurenson & Caro 1994).

Most studies on handling and capture effects focus on small mammals and birds, with few examining the effects of handling on large mammals, especially large game species (Withey *et al.* 2001). However, all animal captures will involve stress and some risk of injury or mortality. Also, the effects of handling will vary with species, geographical location, capture protocol and personnel. It is therefore important to evaluate the impact of each capture and handling study whenever possible.

We assess the long term effect of chemical immobilization on African buffalo *Syncerus caffer* (Sparrman, 1779) in the Kruger National Park (KNP), South Africa, with regard to the effects on delayed, post capture mortality and female calving rates. Capture

protocols are available for most Southern African game, including buffalo (see Harthoorn 1990, McKenzie 1993, Kock *et al.* 2006). The well researched capture and immobilization technique and experienced staff result in direct anesthetic mortalities being reduced to minimal levels. However, although these direct capture mortalities can be controlled for, it is important that the potential long term effects of capturing should also be addressed. Mortality associated with capture may not be immediate and capture-related mortality will therefore be underestimated if animals are not monitored after release. Post-release mortality may remain a factor, with predation an important component of mortality for buffalo (Funston & Mills 2006). The strong dependence of buffalo on herd defense against predators (Pienaar 1969, Sinclair 1977) may increase predation rates on isolated captured individuals.

The main risks of direct capture deaths may also contribute to post-capture mortality. Immobilized buffalo, and especially pregnant females, are susceptible to hyperthermia, particularly after long darting chases at high ambient temperatures (Meltzer *et al.* 2006). Death can occur if body temperature exceeds 43°C (Meltzer & Kock 2006), alternatively hyperthermia may lead to rumen stasis, followed by loss of body condition (R. Bengis, personal communication). Buffalo that go down in lateral recumbency may also bloat, frequently regurgitating rumen contents which may be aspirated into the trachea and lungs (Meltzer *et al.* 2006). Aspiration of rumen contents during regurgitation may result in direct death as a result of asphyxiation, or may cause delayed post capture death up to a few days to weeks after capture through foreign body pneumonia (Meltzer *et al.* 2006). Increased stress levels in helicopter chased buffalo have been reported (Hattingh *et al.* 1984). It is however, uncertain if this predicted acute stress induced will have any long term negative effects. Capture myopathy (overexertion and exhaustion), associated with physical exertion and stress during capture is the primary cause of concern in many artiodactyl handling operations. Although capture myopathy may occur under certain circumstances, buffalo are not generally highly susceptible during field immobilization and release programs (Bengis 1993). Capture myopathy may however, easily go undetected, and deaths resulting from tissue damage may occur up to two months after capture (Meltzer *et al.* 2006). Buffalo cows rarely abort in the field (Bertchinger 1996), or even when captured in buffalo breeding programs (R. Bengis,

personal communication), but captures during critical phases of gestation may elevate the risk of abortion. Also, calves separated from cows and the herd, especially in the suckling period, may result in increased calf mortality.

This study is conducted at the end of a larger research program, the Buffalo TB Project which investigated the epidemiology, disease dynamics and ecological consequences of bovine tuberculosis (bTB, *Mycobacterium bovis*) in African buffalo in KNP. The recent Buffalo TB Project employed non-lethal sampling methods to study ecological questions about primarily disease dynamics, bTB and buffalo interactions and lion-bTB interactions (e.g. Caron *et al.* 2003; Cross *et al.* 2004; Tambling 2004; Cross *et al.* 2005a; Cross *et al.* 2005b, Cross & Getz 2006). Radiocollaring and bTB prevalence tests, and consequently chemical immobilizations, formed an important part of the study.

The current study is an opportunistic attempt to assess capture effects on buffalo, facilitated by the detailed long term observations made during the research project study period. Our motivation is therefore to evaluate the captured buffalo sample as representatives of the total buffalo population. Since the captured animals are forming the base line for other studies on population demographics, it is crucial that they are a representative sample, and that captures do not interfere with survival or reproductive probabilities. Because these animals are often immobilized, we need be able to separate possible capture effects from bTB effects, a main research question. Additionally, with the research being conducted in a National Park, and with growing public awareness of animal welfare issues, this study presents important findings to facilitate further research. The majority of the mortality analyses are on the hidden effects of capture that may contribute to mortality after the animal have been released, and capture effects on calving rates of buffalo cows. Direct capture deaths are discussed but not included in the post capture survival analyses.

MATERIALS AND METHODS

Study area

Kruger National Park lies on the North Eastern border of South Africa and Mozambique, between latitudes 22°19' and 25°32'S and longitudes 30°52' and 32°03'E. It is one of Africa's largest protected areas, and South Africa's largest national park,

covering 20,000km² (Rodwell *et al.* 2000). Private game farms surround much of the western boundary and add another 220 000ha to KNP (De Vos *et al.* 2001). The substrate in the western half of the park is granitic, while the eastern half is mainly basaltic clay. Mean annual rainfall follow a north-south gradient, increasing from 400mm in the north to 700mm in the south (Gertenbach 1983). The southern parts of KNP are dominated by mixed *Combretum* woodland and thickets. The central region is characterized by mixed *Combretum* woodland, *Acacia nigrescens* and *Sclerocarya birrea* savanna depending on substrate. Field data were obtained from herds around the Satara and Lower Sabie Regions. The Satara region, from which the majority of the data were collected, contained 4-12 buffalo herds and roughly 3000 buffalo during the study period (Fig. 1).

Data

Field data were collected by project field staff based in KNP. A total of 881 buffalo captures or recaptures were made between 13 November 2000 and 28 November 2005. The number of unique individuals captured was 593, with 288 recaptures. From these, 507 captures and 235 recaptures, took place in the Satara region, and 86 captures, 53 recaptures near Lower-Sabie. A total of 572 buffalo captures were made from helicopter and 309 during ground captures.

Radiocollaring of buffalo during immobilization enabled accurate monitoring of survival and reproductive performance in the field. Radiocollared buffalo were re-sighted on foot and from vehicles throughout the study period from distances ranging from 50 to 1000m, usually two to three times per week while monitoring buffalo herds. Whenever an individual was not sighted for a one month period it was located from air by fixed-wing aircraft. Annual rainfall records for the study period were obtained from the Satara weather station (N. Zambatis unpublished data). Annual rainfall was calculated over the seasonal cycle, from August to July.

Capture procedure and radiocollars

Buffalo were darted from the ground (individual sampling) or by aerial darting where up to 14 individuals (10.4 ± 0.43 , mean \pm S.E.) are immobilized together, using a Eurocopter Colibri EC120. Ground darting phases lasted $24:00 \pm 4.05$ minutes ($N=15$,

mean \pm S.E.) and the helicopter darting period $11:40 \pm 0.97$ minutes ($N=46$). The mean times that buffalo spent immobilized was $12:53 \pm 0.43$ minutes ($N=264$) in ground captures and 49.43 ± 2.29 minutes ($N=43$) during helicopter captures. Captures were conducted throughout the year and restricted to early mornings. Kruger National Park's own aluminum darting system (4 ml darts, each fitted with a 45mm collared needle, fired from a modified 20 gauge shotgun) was used. Dosage is approximately 8mg etorphine hydrochloride (M99; Logos Avet) and 100mg azaperone tranquilizer (Stresnil; Janssen Pharmaceutica) for adult bulls and 7mg etorphine hydrochloride and 80mg azaperone for adult cows. Anesthesia is reversed by intravenous administration of diprenorphine hydrochloride (M5050, Logos Avent). Numerous measurements were taken during capture, including body and horn length, fecal and blood samples.

Selected individuals were fitted with radiocollars based on the needs of various research projects. Representative age and sex classes were collared. VHF (MOD-600 transmitter, Telonics, 932 E. Impala Av., Mesa, Arizona, 85204-6699, USA) and GPS collars (CBU-308, African Wildlife Tracking, 18 North Street, Rietondale, Pretoria, RSA) were used. Collars consisted out of a GPS/Satellite transmitter encapsulated in a plastic vessel of dental acrylics with a three plied PVC belting collar fitted around the neck. The collars weighed *ca.* 1.9kg, which is $<1\%$ of an adult buffalo's body weight, and were not likely cause physical trauma, pain, inhibition of movement or prolonged stress responses which may be able to decrease immunity (Sapolsky 2000).

Data analysis

Delayed mortality

We restricted analysis to data on radiocollared buffalo collected from January 2001 to February 2006 (61 months). Individuals fitted with radiocollars are usually found soon after death, before carcasses are totally destroyed, while un-collared individuals are usually located longer after death, if at all. This decreased the sample size, but increased the probability of recording mortality thereby increasing the accuracy. Radiocollars were fitted on 166 individuals, the majority of which were captured in four helicopter sessions in November 2000 ($N=6$), April 2001 ($N=27$), August 2001 ($N=51$) and November 2001 ($N=12$) while the remaining collars were fitted throughout the study period during

individual ground captures. Sixty-two radiocollared buffalo died during the study period. Buffalo fitted with collars but that died during recaptures ($N = 4$) are excluded in the generalized linear modeling investigating post release mortality. The mortality date was taken as the day the buffalo was found corrected with an estimated time since death (range 0-30 days). Causes of mortality were determined by circumstantial evidence or direct observation. Mortality data were analyzed using multiple competing hypotheses in logistic regression analysis.

Analysis was based on generalized linear models where the survival over a seasonal interval was modeled as a function of different explanatory variables. Analyses were performed in SAS 9.1 (PROC LOGISTIC; SAS Institute 2003). Each individual buffalo was first represented in the season of the first capture, and then in all subsequent seasons up to its death or the end of the radiocollared period. This analytic design made the assumption that survival in season two was independent of season one for individual animals. To attain a strict independent data set would have required a large amount of available data on repeated captures of individuals to be censored. The added complexity of unequal number of immobilizations of individuals, and different study periods prevented the use of conventional repeated measures analysis. Consequently, we accepted the potential bias and risks associated with autocorrelation and included all the data on capture events. The analyses may be biased towards persistent individuals (those with lower hazard functions and thus better survival), especially in the latter parts of the study period as individuals with high hazard functions die early, and contribute less to the overall model. Lack of independence between observation periods may underestimate the variance of mortality estimators, but are unlikely to influence the parameter estimate itself (McCullagh & Nelder 1989). However, the potential bias is not unique to this study (see for example Tuyttens *et al.* 2002, Engelhard *et al.* 2002). All radiotelemetry survival studies make the assumption that observation periods of individual animals are independent (in this case season one and season two), although violation of this assumption is generally inevitable (Winterstein *et al.* 2001). A degree of bias is also unavoidable in nearly all restricted mortality rate estimate methods (life tables and survival analyses) with a heterogeneous sample, as the sample structure is inexorably modified as individuals die (Zens & Peart 2003).

Factors affecting survival: model fitting

The response variable modeled was the binary outcome “*dead or alive*”, with death recorded as an event. Previous studies have identified several factors which affect buffalo survival, including sex, age, and rainfall (Sinclair 1977, Funston & Mills 2006), so these variables formed the base of our *a priori* model set from which our objective was to assess whether any capture variable influenced the probability of survival. Model selection methods were based on Akaike information criterion (AIC) (Akaike 1973, Burnham & Anderson 2002). Information theory offers an alternative to traditional probability based analysis, especially in a multiple working hypotheses scenario. AIC is based on Kullback-Leibler information and maximum likelihood (Anderson *et al.* 2000, Burnham & Anderson 2004) and estimates the relative information loss when fitting a particular model compared to other plausible models, with better models losing less information. AIC is defined as $AIC = -2 \log(L(\hat{\theta} | \text{data})) + 2K$ where $\log(L(\hat{\theta} | \text{data}))$ is the value of the maximum log-likelihood estimate given the data over the unknown parameters $\hat{\theta}$. K is the number of parameters in the model ($K + 1$ for logistic regression models [Anderson & Burnham 2002]).

The model with the lowest AIC provides the best fit for a particular data set. Basing model selection on AIC values is justified as AIC incorporates both assumptions of model selection: goodness-of-fit and parsimony. By incorporating the number of model parameters in calculation, AIC essentially penalizes models for having more parameters (i.e. more complex models need to explain the data better in order to be considered meaningful). AIC has an advantage over the likelihood ratio test as it allows all models, even the non-nested ones, to be compared.

A set of competing models was developed *a priori*, as the results depend on the relative support for each model. The *a priori* selection of biologically relevant models (hypotheses) sidesteps the pitfalls associated with inference drawn from a ‘single best model’ derived from traditional *p*-value orientated analyses. We corrected AIC values for each model for sample size (AICc). The AICc algorithm, with n the sample size, is $AICc = AIC + (2k(k + 1))/(n - k - 1)$ (Anderson *et al.* 2000). Models were ranked against one another based on the $\Delta AICc$ values of each model, relative to the best model [$\Delta_i = AIC_i - AIC_{\min}$] (Burnham & Anderson 2002). This conversion forces the best model to have

$\Delta\text{AICc} = 0$, while the rest of the models have positive values. The amount of the decrease in the overall AICc value is indicative of the strength of evidence for whether or not the factors or interactions in the model should be kept (Burnham and Anderson 2004).

The likelihood of the each model given the data $L(g_i|\text{data})$, $[\exp(-\Delta_i/2)]$ for $i = 1, 2, \dots, R$, and the Akaike weight (w_i) of each model i among r potential models was calculated $[w_i = \exp(-\Delta_i/2) / \sum_{r=1}^R \exp(-\Delta_r/2)]$ (Burnham & Anderson 2002). Akaike weights represent the relative weight (importance) of each model calculated, where ΔAIC_i is the ΔAIC of model i . and the denominator is the sum of all delta AICc's in the set of models. The sums of all the weights equals 1 and you can consider w_i as the weight of evidence for model i being the best model. A set of models can be ranked according to the Akaike weights, after which inference should be based on the set of models, rather than the highest ranked model only. This is especially important when a number of models have similar weights, or when the highest ranked model has a moderate weight. Models within $\sim 2 \Delta\text{AICc}$ of the best model show considerable support while those more than $\sim 7 \Delta\text{AICc}$ is really weak compared to the best model. All models in the model set were used in model averaging (Burnham & Anderson 2002). The weighted model average, calculated for each parameter in the model averaging dataset equals

$$\hat{\beta}_j = \frac{\sum_{i=1}^R w_i I_j(g_i) \hat{\beta}_{j,i}}{w + (j)}$$

$$w + (j) = \sum_{i=1}^R w_i I_j(g_i)$$

where

$$I_j(g) = \begin{cases} 1 & \text{if predictor } x_j \text{ is in model } g_i \\ 0 & \text{otherwise} \end{cases}$$

B_j is the coefficient of parameter x_j in model g_i . The B coefficients of the parameter x_j are multiplied by the Akaike weight of the respective models in which it occurs, and the outcome of each model calculation for parameter x_j is summed. The sum total is then

divided by a modified Akaike weights sum in which that parameter occurs. Standard errors for each of the model averages was calculated by converting the variance estimator

$$\text{var}(\hat{\theta}) = \left[\sum_{i=1}^R w_i \sqrt{\text{var}(\hat{\theta}_i | g_i)} + (\hat{\theta}_i - \hat{\theta})^2 \right]^2$$

to standard errors $\hat{s}_e(\hat{\theta}) = \sqrt{\text{var}(\hat{\theta})}$.

Model averaging procedure based on w_i values of a number of models incorporates model selection uncertainty by computing average estimates for parameters of interest across multiple models in which that parameter occurs (Burnham & Anderson 2002). Summing the w_i for all models in which the parameter of interest occur, permit multi-model inference based on the entire set of candidate models, rather than the single best model with the lowest AIC value $[\hat{\theta} = \sum w_i \hat{\theta}_i]$ (Burnham & Anderson 2001). We were interested whether or not models with the capture associated variables included, ranked within $\sim 2 \Delta\text{AICc}$ of the highest ranked model.

The strength of evidence of parameter estimates were evaluated by the degree to which the 95% confidence intervals ($\hat{\beta} \pm 1.96 \cdot \text{S.E.}$) of parameter estimates overlapped zero. Parameter confidence intervals that overlap zero suggest the variable may not have a significant influence on the outcome variable. Survival estimates were calculated during the six month seasonal data interval where survival (\hat{S}) = $\exp(\hat{\beta}_0 + \hat{\beta}_1 + \dots + \hat{\beta}_k) / (1 + \exp(\hat{\beta}_0 + \hat{\beta}_1 + \dots + \hat{\beta}_k))$ with $\hat{\beta}_0$ the intercept estimate, and $\hat{\beta}_1 - \hat{\beta}_k$ parameter estimates of non-intercept parameter levels.

The ΔAICc estimates are indicators of relative model fit. However, the highest ranked model may still be a weak model if the whole model set poorly fit the data (Greaves *et al.* 2006). We assessed the goodness-of-fit of the highest ranked survival model and the global *a priori* reproductive model, and estimated overdispersion (\hat{c}) from the Pearson *Chi* square statistic ($\hat{c} = \chi^2/\text{df}$; Lebreton *et al.* 1992, Cox & Snell 1989). If overdispersion is present in the data, the goodness-of-fit statistic will typically exceed its degrees of freedom (Burnham & Anderson 2002). The survival analyses lacked a single

global model; therefore we partitioned the model set into subsets, each with its own subglobal model (Burnham & Anderson 2002). The computed \hat{c} estimates of subglobal models indicated adequate fit and no overdispersion (highest ranked subglobal model with $\chi^2 = 19.68$, $df = 21$; $P = 54$; $\hat{c} = 0.94$). The global reproductive model presented no indication of lack of fit ($\chi^2 = 104.45$, $df = 100$; $P = 0.36$) or overdispersion ($\hat{c} = 1.04$). When modeling criteria is based on Kullback-Leibler information, parsimonious a priori models will fit when the global model fits, eliminating the need to test each model independently (Anderson & Burnham 2002).

Explanatory variables

The following class variables were used in the analyses with the number of levels given in parentheses. Two way interactions of some variables were also considered.

1. *Year (yr)* (5) of the specific entry, from 2001 to 2005. The first six captures in November 2000 were excluded from the analyses.
2. *Season (seas)* (2), divided into a 'wet' and 'dry' season, with the state of the response variable assessed at the end of each season. Dry season was specified as 1 August to 31 January, and the wet season 1 February to 31 July. This is the most biologically relevant division as buffaloes' body condition is generally the worst in the period from August to January (P.C. Cross, unpublished data).
3. *Sex (s)* (2) records male or female.
4. *Age (a)* (4) is classified as 1-3 years (calves and juveniles), 4-5 years (young adults), 6-8 years (adults) and >8 years (adults). Ages were determined by incisor eruption patterns for those individuals under five years old (Pienaar 1969, Grimsdell 1973, Sinclair 1977) and by general visual assessment in mature animals.
5. *BTB (tb)* (2) indicates the BTB status of the buffalo based on the last available test results. BTB status was determined by a modified gamma-interferon (IFN γ) BOVIGAMTM assay (Wood and Jones 2001). BTB negative individuals were retested at six or 12-month intervals.

6. *Capture (c)* (2) indicates whether the buffalo was captured during the last three months of any season which it survived, or within the three months prior to death.
7. *Capture-lag (clag)* (2) indicates a lag period of 3 months excluding the capture time recorded above, i.e. records whether the buffalo was captured during the first three months of any season which it survived, or captured within three to six months prior to death.
8. *Capture Method (cmet)* (3) specifies the capture method, (helicopter-, ground capture, or not captured) used in the corresponding capture entry. We predicted that helicopter captures might have a greater effect as the helicopter chase result in greater herd scatter and isolation of captured individuals. Also, the energetic consequences of running for a 15 minute period may be considerable, especially in bTB positive animals with less than 100 % lung function.
9. *Immobilizations (i)* (4) records the number of times an individual was captured at the end of the specific season, classified as one, two, three and four to six times.
10. *Drought (d)* (2) subsets the year variable into two categories, drought and no drought. We define drought according to Funston (1999) where drought conditions occur when rainfall is less than 75% of the mean annual precipitation. The long-term (1933-2002) mean annual rainfall for the Satara rainfall station was 519mm per year (Tambling 2004). We subset only the second drought interval in the study period, August 2002 – July 2003. This period received the lowest rainfall (324.9mm), and is the second of two consecutive drought years (August 2001 – July 2002, 338.8mm).
11. *Drought-lag (dlag)* (2) refers to a six month delay period since the August 2002 – July 2003 drought, allowing partitioning of the dry season of August 2003 to January 2004 versus all other time periods. We predict that buffalo will be in their worst condition during this dry season of the study period since it follows two successive drought years.

Reproduction

The female buffalo reproductive cycle is well documented. The estrus cycle (23 days) is limited to March to May, resulting in well defined seasonal calving restricted to

the summer months (Pienaar 1969). In KNP, calving is primarily restricted to January - April, with a peak in births during January and February (Fairall 1968). The age of first calving normally range from 4 to 5 years (Pienaar 1969). Gestation is 340 days, after which a single calf is born (Vidler *et al.* 1963). The inter-calving interval (ICI) under optimal conditions is 14.1-16.1 months, with a 75% pregnancy rate among adult females (Sinclair 1977), but under suboptimal conditions cows only calve every second year (Pienaar 1969). Female age (Sinclair 1977, Rodwell *et al.* 2001), geographical region (central or southern zone, Rodwell *et al.* 2001) and possibly bTB status (Jolles 2004, but not in Rodwell *et al.* 2001) are important factors governing fecundity. Low rainfall has severe effects on both fecundity (Sinclair 1977) and calf survival (Pienaar 1969). As a result these variables were included as explanatory variables in most *a priori* models.

Factors affecting reproduction: model fitting

The calving success of 172 buffalo cows ($N = 348$) was recorded from 2001 to 2005, and include data on both captured cows ($N = 227$) and cows that were known, but never captured ($N = 121$). The response variable modeled was an index of calving rate, (calves/cow/annum), that indicates whether the cow had a calf (=1) or if no calf was recorded (=0). Calving success was determined by visual sightings of cows with calves, observed at various times throughout the season. Females were considered to have reproduced successfully when a calf was seen once or more in association with that female. However, when a female was seen once with a calf, but no calf was seen at two or more equations, no calving was recorded. Fecundity and calf survival could not be separated, and although our definition of calving rate may be depressed by unobserved calf mortalities, we do believe it to be an unbiased index with respect to the effects of capture. If captures do seem to have an influence on the measured calving rate, further analysis or studies may attempt to differentiate between birth rates and calf survival. We were primarily interested in the effect of capture on calving rate, but had to correct estimates for the influence of rainfall, female age and geographical location. We predicted that if capture did have a negative effect, pregnant females are likely to be most susceptible during the last trimester and calves during first couple of months following birth. We assumed that captured females and females that were not captured had the same

bTB prevalence since the bTB status of only captured cows were known. We furthermore assumed serial data entries of single females to be independent between different reproductive years.

The data were analyzed with logistic regression in an information-theoretic approach as detailed above, to select the best models and to average parameter estimates. The strength of evidence of parameter estimates were evaluated by the degree to which the 95% confidence intervals ($\hat{\beta} \pm 1.96.S.E.$) of parameter estimates overlapped zero. Estimates of calving rate over the annual data interval were calculated, where calving rate (δ) = $\exp(\hat{\beta}_0 + \hat{\beta}_1 + \dots + \hat{\beta}_k) / (1 + \exp(\hat{\beta}_0 + \hat{\beta}_1 + \dots + \hat{\beta}_k))$ with $\hat{\beta}_0$ the intercept estimate, and $\hat{\beta}_1 - \hat{\beta}_k$ parameter estimates of non intercept parameter levels.

Explanatory Variables

The following variables, with the number of levels given in parentheses, were used in developing generalized linear models of reproduction. Two way interactions between *year* and *age* were also considered.

1. *Year* (*yr*) (5) represents the year of recorded calving. The year variable is used as index of annual rainfall that may influence food availability and subsequently buffalo body condition.
2. *Age* (*a*) (3) records the cow's age category at the reproductive record. Only females older than 5 years of age were included in analysis, and females are grouped in three age classes: 5-8, 8-12 and 12+ years of age. In most instances the female's birth year was known, while some females were aged by general visual assessment.
3. *Herd* (*h*) (2) corresponds to the location of the female in either the Satara (central region) or Lower Sabie (southern region) herds.
4. *Immobilizations* (*i*) (4) are the number of immobilizations before the recorded reproductive year (zero, once, twice or three to six times).
5. *Capture month* (*c*) (5) specified when the female was last captured. For each case line, was the female captured:

- a. in the late gestation period (November – January) before the reproductive event (possible calf loss due to abortion)
- b. in the post parturition period (February – April) after the reproductive event (possible calf loss due to predation)
- c. in the middle of the gestation period (April to October)
- d. the last capture was outside the current reproductive cycle
- e. she has never been captured

Following the computation of the *a priori* model set parameter estimates, another four models were constructed *a posteriori* and included in a post hoc table. The additional models contained a *drought* (*d*) or *drought-lag* (*dlag*) variable instead of the year of recorded calving. The *drought* variable partitioned the calving rate of 2002 and *drought-lag* the calving rate of 2003 from all other study years. New averaged parameter estimates were calculated for the *a posteriori* model set.

RESULTS

Direct Mortalities

Direct capture death mortalities were much lower (6 deaths in 881 captures, 0.68% mortality rate) than the 2% upper limit recommended by Arnemo *et al.* (2006). Four animals died as direct consequence of immobilization, due to regurgitation of rumen contents and subsequent suffocation. One animal was euthanized after it failed to stand up after drug reversal. One animal, which was not immobilized, attacked staff and was shot. The four buffalo fitted with radiocollars but that died during recaptures are excluded from the analysis of post capture survival.

Delayed Mortality

The *a priori* models used in analyses (Table 1) are ranked according to the Akaike weight of support for each model. The highest ranked model has *season*, *capture*, *age*, *sex* and the *age*sex* and *season*capture* interactions as explanatory variables. However, this model only has a w_i of 0.38 as strength of evidence of being the best model, giving

good reason to exercise multi-model inference. The second ranked model ($w_i = 0.31$) contains the effect of the capture method on survival instead of the *capture* variable and the *season*capture* interaction. This is the only model within 2 ΔAICc from the highest ranked model. These two models can be considered the most parsimonious models important in explaining mortality. Models within 7 ΔAICc of the best model include *capture*sex* interaction (model 4), *bTB* (model 5), *drought-lag* (model 6), *drought* (model 7), *capture-lag* (model 8) and *year* (model 10). Although these models still indicate useful variable combinations in explaining the variance in the response variable ($< 7 \Delta\text{AICc}$), they exhibit much lower support than the best two models ($w_i \leq 0.07$).

No model parameter showed considerable strength of evidence as all parameter estimates had 95% confidence intervals that overlapped zero to some extent. The odds ratio (ψ) ($\psi = e^\beta$) quantifies the relative measure of the odds of success (the ratio of the probability of a success to the probability of a failure), in one group relative to another (Collett 2003). Parameter estimates followed predictions and indicated that males had greater risk of death than females ($\psi = 2.13$, 95% CI: 0.66 to 6.85), the youngest and oldest age classes had the highest likelihood of death (ages 4 -5, $\psi = 0.23$, 95% CI: 0.03 to 1.98; ages 6-8, $\psi = 0.92$, 95% CI: 0.26 to 3.21; ages >8, $\psi = 2.31$, 95% CI: 0.77 to 6.97), and mortality was most probable in the dry season ($\psi = 1.99$, 95% CI: 0.91 to 4.36), especially the dry season following the two year drought (*drought-lag* $\psi = 1.33$, 95% CI: 0.75 to 2.37) (Fig. 2). The drought period from August 2002 – July 2003 did not result in increased likelihood of mortality ($\psi = 0.81$, 95% CI: 0.53 to 1.24).

Support is present for a capture effect on survival as models with the *capture* variable or capture-effect interaction have lower AICc than models without the variable. However, when the *capture* parameter estimate effect is evaluated by the degree to which the 95% confidence intervals of parameter estimates overlap zero (Table 2), a weak effect is indicated ($\hat{\beta} = 0.18$, 95% CI: -0.82 to 1.17), although buffalo tend to be more susceptible to death in the three months after capture. Recently captured buffalo have an odds ratio of 1.19 (95% CI: 0.44 to 3.23) relative to buffalo not captured, suggesting greater probability of mortality although the confidence intervals indicate some uncertainty. Other capture related parameters with the greatest magnitude of effect

(although overlapping zero) is $season*capt$ ($\hat{\beta}=1.56$, 95% CI: -0.86 to 3.99) and $captmethod3$ ($\hat{\beta}=1.70$, 95% CI: -0.90 to 4.29). $Season*capt$ assumes survival is the same across wet and dry seasons for buffalo not captured, but that survival is different between seasons for captured buffalo. The positive parameter estimate suggests that captured buffalo may be more susceptible to capture effects in the dry season. Helicopter captures ($captmethod3$) may also increase the probability of mortality compared to ground captures ($captmethod 2$) or no captures. Ground captures have an odds ratio of 1.43 (95 % CI: 0.69 to 2.94) relative to no captures, while the odds of death increase 5.64 times (95% CI: 0.41 to 73.31) for helicopter captured buffalo versus individuals not captured. However, the three to six month $capture-lag$ period did not show a relationship with increased mortality ($\psi = 0.51$, 95% CI: 0.14 to 1.87). The probability of mortality in the three months since capture was also lower for the repeated captures of individuals (second to sixth immobilization)

Survival estimates

Seasonal survival (\hat{S}) estimates for males and females of the four age categories were calculated (Fig. 3). Males have lower survival than females in all age classes, especially in males older than 8 years. Survival was better during the ‘wet’ season (February – July), and male survival also decreased more than female survival in the dry season ($\hat{S}_{(>8y\ male)} = 0.79 - 0.82$; $\hat{S}_{(>8y\ female)} = 0.89-0.91$). The intermediate age categories, 4-5 and 6-8 years had the best survival. Captured buffalo have lower survival for all sex and age classes, but the effect was weak. For both males and females, capture do not decrease survival by more than 0.01 for age classes 1-3, 4-5 and 6-8. Age class >8 show the greatest response to capture, with dry season survival rate dropping by 0.03 to 0.79 for males and by 0.02 to 0.89 for females.

Reproduction

The highest ranked model, consisting of the *year*, *age* and *capture month* variables has a w_i of 0.58 (Table 3). The only other competitive model to rank within two $\Delta AICc$ of this model is obtained by dropping the *age* variable. All other models have considerably less support of being the best model ($w_i < 0.05$). Support for a *year* and

capture effect on calving rate is signified as the univariate *year* model ranks third, and models including the *capture month* variable as parameter have lower AICc values than models without the variable. The inclusion of *herd*, *number of immobilizations*, and the *year*age* interaction decrease the fit of the model, resulting in higher AICc values.

Three *a priori* model set parameter estimates, *year3* and the *capture* categories *c1* and *c2* (females captured between November and January, and May to October) (Table 4) exhibit substantial evidence as explanatory variables as their 95% confidence intervals did not overlap zero. Confidence intervals of all other parameters included zero, suggesting that they have a weaker influence on calving rate. Females captures between November and January (*c1*) had nearly five times the odds of a calf recorded ($\psi = 4.99$, 95% CI: 1.39 to 17.91) relative to females that were never captured, while those captured from May to October (*c2*) also had greater probability of successfully reproducing ($\psi = 2.76$, 95% CI: 1.06 to 7.18) relative to females that were never captured.

Equally, females captured from February to April (*c3*) ($\psi = 1.65$, 95% CI: 0.70 to 3.89) and those last captured outside the current reproductive cycle (*c4*) ($\psi = 2.07$, 95% CI: 0.80 to 5.38) also exhibited higher calving rate ratios relative to the non-captured females. However, confidence intervals for *c3* and *c4* overlapped zero, thus uncertainty is associated regarding the strength of these parameters. The *immobilization* parameters all overlapped zero, but supported higher calving rate in captured females. Age category odds ratios suggested the highest calving rate in females >12 years old (*age1*, $\psi = 0.47$, 95% CI: 0.18 to 1.22; *age2*, $\psi = 0.74$, 95% CI: 0.38 to 1.43), but parameter estimates also overlapped zero.

The considerable reduction in calving rate in 2003 (*year3*) ($\psi = 0.19$, 95% CI: 0.07 to 0.51) lead to the *a posteriori* model set including the effects of the drought of 2002. The post hoc analysis caused the model containing the *drought-lag*, *age* and *capture month* variables to rank the highest ($w_i = 0.63$), and this was the only model with considerable support. The previous best supported model (*year + age + capture month*, $w_i = 0.14$), the new model *drought-lag* ($w_i = 0.12$), and the *year + capture month* model ($w_i = 0.07$) ranked within 7 Δ AICc from the best model. No other models were competitive.

Parameter estimate confidence intervals averaged over all the models in the post hoc model set suggest that the *capture month c1* parameter ($\psi = 4.49$, 95% CI: 1.26 to 16.04) and *drought-lag* parameter ($\psi = 6.69$, 95% CI: 1.42 to 31.45) (Fig. 4) have a significant influence on calving rate, as these confidence levels do not overlap zero (Table 6).

Calving rate estimates

The annual calving rate of the *drought-lag* year (2003) was compared with all other years, with subset results for female age and capture histories. Reproduction was markedly lower in 2003, with a mean calving rate of only 0.20 across female age and capture history compared to the mean calving rate of 0.61 in all other years, as predicted by model coefficients. Older female age categories had higher calving rates in all years. In contrast to our predictions, females captured in their gestation period showed higher calving rates. This was most evident for females captured just before parturition, from November to January (model predicted calving rate of 0.17-0.84). Females captured in the months after the birth peak (February to April) had the same calving rates than those captured outside the gestation period. In five out of the six categories, females never captured recorded lower calving rates (Fig. 5).

DISCUSSION

Capture deaths

The small sample of five animals that died on the ground during captures makes inference rather speculative, if not optimistic. Two males and three females died during captures. One cow died in July during a ground capture, and two cows died during October during helicopter captures. All three females were pregnant. Heavily pregnant females are more susceptible to hyperthermia, acidosis and regurgitation of rumen contents. The large gravid uterus presses on the gut contents which press forward on the diaphragm, amplifying the risk of regurgitation (Bengis 1993). However, cows should not be 'heavily pregnant' by October, and the fact that all three females were pregnant might have been a chance outcome. Both male buffalo died during helicopter captures.

Helicopter captures therefore seem to increase the possibility of direct capture death. This may be expected, as more individuals are captured at the same time, with increased buffalo activity during darting periods, and longer time on the ground. However, the low proportion of overall capture deaths is acceptable from an ethical and veterinarian perspective regardless of the perceived increased risk.

Delayed mortality

Our survival models are simple hypotheses developed to determine if a relationship exists between capture and mortality. Because survival will additionally depend on an array of other unidentified or unmeasured hazard factors, our analyses should not be seen as an attempt to quantify demographic responses. The proximate cause of mortalities was lion predation (64% of mortalities recorded as lion predation, 7% other, and 29% unknown); although in some instances lions may just have scavenged a carcass that died from other causes. With lion predation the primary cause of natural mortality, we can only speculate that deaths within three months of a capture were capture-related, even though we have no physical evidence to support such a statement. Although the radiocollars did not seem to cause physical injury to buffalo, some males got their horns stuck under another male's collar during fighting, and three buffalo were recorded with a front leg caught in a loose collar, resulting in the predation of one of these by lion. Even though these individuals were negatively affected by wearing a collar, radiocollars were considered to present no further risk to the other buffalo in the sample. Carrying radiocollars has been shown to adversely effect some species (e.g. studies cited in Withey *et al.* 2001), but these effects are generally seen in smaller species where the radiocollar represents a more significant percentage of the animal's total body weight.

Mortality-parameter relationships abide by conventional predictions, with mortality positively associated with the juvenile and oldest age categories, males and dry seasons. In addition, delayed mortality does seem to be positively related to captures, especially helicopter captures. The inclusion of the *capture* variable in models results in better fit to the data than for those models without the variable. However, it is impossible to draw infallible conclusions from the parameter estimates with confidence intervals overlapping zero. The wide confidence intervals indicate that there was little power to

detect important factors affecting survival, brought about by the small initial sample size and fairly low mortality rate during the study period, resulting in fewer statistical ‘events’.

The influence of capture is much smaller than those of season, sex, and age. While the odds of death double in dry seasons opposed to wet seasons, for males versus females and old animals relative to juveniles, capture only result in a slight increase in the odds of death. In six out of sixteen categories incorporating the *age*, *sex*, *season* and *capture* variables, *capture* did not lead to a decrease in survival. In males, only the oldest age category show decreased seasonal survival rates of the captured class more than 0.01, with a decline of 0.02 in the wet season and 0.03 in dry season. The only female cohort where the captured cohort’s survival rate decreases more than 0.01 is dry season females older than eight years, with a 0.02 decrease in seasonal survival rate compared to not captured females. The oldest age categories are therefore more susceptible to capture effects, even though these declines may be minor.

However, when seasonal survival rate variance and model uncertainty are considered, the decrease in seasonal survival of captured individuals becomes negligible, as variance will remove the difference between captured and not-captured survival rates. Additionally, even though capture effects (for example foreign body pneumonia and rumen stasis leading to condition loss) may take weeks to manifest (Meltzer *et al.* 2006), it is likely that the three month interval allocated to capture related mortality will overestimate the effects of capture by including some mortality that would have occurred in the absence of capture. If this added uncertainty about capture’s influence on mortality in the capture data interval is taken into account, the decline in survival rate of captured individuals becomes unimportant at a population level. With overall capture effects negligible, the weight of influence of interactions between capture and season and differences between ground and helicopter captures diminishes.

The majority of capture-effect studies on ungulates find that chemical immobilization and radiocollaring do not significantly affect survival probabilities (e.g. Ballard *et al.* 1981, Berger *et al.* 1983, DelGiudice *et al.* 1986, Larsen & Gauthier 1989, Côté *et al.* 1998). Immobilized male bison (*Bison bison*), for example, showed reduced, but insignificant decline in over-wintering survival compared to bison not captured

(Berger & Kock 1988). Similar small scale declines in survival rate following chemical immobilization have been reported for several other species (e.g. Cypher 1997, Johannesen *et al.*1997). Our results are comparable with these, and suggest that captures should not be a major determinant of survival in future capture programs if risks are limited to present levels.

Reproduction

Calving rate of females is best described by the combined effects of low rainfall, female age and capture history. We believe only rainfall and female age to be real sources of reproductive variability. Captures, although favorably ranked in model selection, more accurately describe the captured sample, rather than contributing to calving rate.

The *drought-lag* variable had the greatest effects on calving rate. The effect of low rainfall on calving rate may be best described by the rainfall occurring in the couple of months prior to conception and throughout the gestation period (Sinclair 1977). Failure of rains, delaying condition gain in the early wet season when conceptions occur may lead to considerable decline in fertility (Sinclair 1977). The low calving rate of 2003 was preceded by only 124.5mm rain from February 2002 – January 2003. The conception months (February – April) received only 16.8mm in 2002, relative to the 627.1mm (2000), 263.1mm (2001), 214.3mm (2003) and 361.5mm (2004) in other years. Female age played a lesser role in explaining calving rate. Still, calving rate tend to increase with female age, with cows older than 12 years showing higher reproductive output in all capture classes in both good rainfall and drought years. The youngest female age category included in the analyses (5 -7 years) had only half the predicted calving rate of old females. The observation that females older than 12 years have the highest calving rates contradict most previous studies, where females aged 8-12 often had the highest calving rates (Bertschinger 1996), but we do not consider these differences to be important.

We predicted that captures might negatively affect buffalo reproduction. In contrast, all captured females exhibited higher calving rates than those known females never captured. Since all captured females were radiocollared during capture, a slight negative calving rate bias may be present between radiocollared females and those never

captured simply due to greater field observation challenges for those females not radiocollared. Even though these individuals were observed at regular intervals, it is much more difficult to locate the known cow with no radiocollar, a reality that may lead to fewer sightings. With high buffalo calf mortality (Funston & Mills 2006), it is possible that more calves of un-collared cows are removed by predators before recorded.

Females captured in the late gestation period (November – January) shows predicted calving rates of 70-80% in good rainfall years, higher than the expected rate. However, captures in this period cannot increase the number of existing pregnancies (calves born in next three months). A possible explanation could be that the amplified recorded calving rate of females captured in the late gestation period might again have been caused by simple observational biases. Observational biases may have arisen if increased surveillance was a feature for those females that were to be captured. Then, if the female was captured around the time she gave birth, there would have been a greater probability of detecting the calf due to more observations than would be the case for females captured in the middle of the gestation period. However, if this was the case, captures in the post parturition period should instead have recorded the highest calving rate. Additionally, there is no evidence of increased observational intensity for females captured around the birth time and those not captured. Averaged observational intensity is standard for all females, regardless of previous or future captures (P.C. Cross unpublished data).

Possibly, captures during this late gestational period is biased to captures of pregnant females. Pregnant females may well be slower runners, or weaken faster, leading to quicker isolation as they lag behind the moving group of animals herded by the vehicle or helicopter, and subsequently increasing the chances of being darted. This ‘capture bias’ possibly apply more to ground captures, where individuals closer in range are often darted. This may even be the case for females in mid-gestation, with evidence provided from the *a priori* model set where females captured in the early to mid gestation period also exhibited slightly increased calving rate relative to other capture categories. If darting is selective for pregnant females, capture deaths risks would be increased during this time of the year. However, the high recorded calving rate indicates that females do

not abort when captured during the last trimester, but carry the pregnancy successfully to parturition.

There is no indication that captures in the post parturition and lactation period decrease that year's reported calving rate. The immediate conclusion may be that captures in this period therefore do not result in reduced calve survival and calving rate. However, negative effects of capture may be masked by two confounding factors. Some females will still be in late gestation during February, consequently artificially inflating the recorded calving rate if selective 'capture biases' apply. Another explanation may be that females who had calved before capture already had the calf recorded (reproduced successfully) before captures took place. The possibility exists that captures may reduce calf survival at a later stage due to separation of the cow and calves during capture. Since we cannot differentiate between fecundity and calf survival, this calf mortality as consequence of capture will go unnoticed. The overall observed calving rate of 0.40 (2001 -2005), or 0.46 (excluding 2003) is lower than previously published rates (e.g. 0.79, Pienaar 1969). This might reflect unobserved early calf mortalities which may reach 30 -70% (Funston 2006), but it is unknown whether captures play any role in elevating this high natural mortality rate.

Small sample size prevented the evaluation of the effect of captures during February, March and April on the next year's calving rate. Captures during the conception season may not lead to lower calving rate even if a cow is to abort due to stress or trauma. Females may have several estrus cycles during a season, thus the possibility exists that a cow which has aborted early in the rutting season may conceive again. It is unknown, but unlikely, that capture stress may actually induce estrous and conceptions to increase the calving rate in the following year (see Tilbrook *et al.* 2000).

The calving rate of females last captured outside the current reproductive cycle may represent the closest approximation to reality. Important though, is that the biases in capture probability proposed above will not bias conclusions of other studies. The increased calving rate of late gestation females do not represent a literal increase in reproductive output as response to capture. This is rather a capture bias, than a reproductive bias. The capture bias is also not likely to violate the assumptions of random sampling. Many of the captures made during the late gestational period would have been

on known animals for bTB prevalence testing or radiocollar purposes, which were first selected and captured during other times of the year.

The calving rates predicted by model parameter coefficients adequately reflect observed calving rates. However, in some cases, small sample size constraints may lead to predicted values different from observed calving rates. Observed calving rates for all females in 2003 is 10% (relative to model predicted 20%), while the observed calving rates for all females in the late gestation period is 64% (contrast model predicted 57%). General trend are however well preserved in the predicted sample (predicted vs. observed calving rates: mid gestation, 0.44 vs. 0.43; post parturition, 0.37 vs. 0.35; outside, 0.39 vs. 0.36; never captured 0.30 vs. 0.32).

Previous studies have found that reproductive success of chemically immobilized females often approach or even exceed that of control females (e.g. Tuytens *et al.* 2002). Reproductive success of immobilized wild horses (*Equus caballus*), is unaffected by field immobilizations (Berger *et al.* 1983), while captive immobilized pregnant white-tailed deer (*Odocoileus virginianus*) show similar reproduction to non-immobilized individuals (DelGiudice *et al.* 1986). However, in some cases reproduction might be adversely affected. Immobilization reduced calving rates in helicopter-darted moose (*Alces alces*) (Ballard & Tobey 1981) and in young mountain goats (*Oreamnos americanus*) (Côté *et al.* 1998). Regular immobilizations of female black rhino (*Diceros bicornis*) also reduced calving rates (Alibhai *et al.* 2001). These might represent cases of species-specific sensitivity to capture effects. Buffalo cows seem to be biologically resilient against abortions in natural conditions, and even when captured during the late gestation period. Capture operations are therefore unlikely to affect the recruitment of young into the buffalo population.

CONCLUSION

This study permits assessment on the long term effect of chemical immobilization on African buffalo population dynamics. The benefits obtained from capturing and radiocollaring buffalo in KNP far outweighs the potential negative effects associated with capture. Although certain individuals may be negatively affected by handling, mainly due

to chance predation, no evidence is presented for large scale adverse effects at a population level. The high efficacy of buffalo captures during the Buffalo TB Project, from both a direct capture death viewpoint and by incorporating delayed, post-release affects on survival and reproduction, can be attributed to the well researched capture protocol and the actions of experienced staff that minimize risk.

Capture effects will be even less important in other studies using this data. It is customary to allow an acclimation phase following the first capture on an individual before including it in the analyzed dataset. Some of the recorded capture related mortalities in this study would consequently be excluded from other studies, with the overall effect of capture on the outcome of these studies insignificant. Even so, the decline in survival rate in the three month period following capture caution that capture-effects should not be dismissed as an a priori assumption in similar types of studies where studied animals are handled, physically captured or immobilized at high frequencies. Censoring those mortalities that occur soon after a recapture would further decrease the chances of capture-related biases.

Captures do not affect female calving rates, but a relationship does appear to be present between captures and calving rates. We recommend that a small correction factor should be included in the analyses of the reproductive data of un-collared females to supplement slight observational biases. Even though the amount of direct capture mortalities is very low, the apparent selective darting of pregnant females does result in increased risk during the late gestation period. We recommend that when possible, adult females should not be captured during the late gestation period or early lactation period (November – April). Captures are generally avoided in these wet summer months, but when females have to be captured during this time for specific research objectives, individual immobilizations during ground captures would be preferred. This will decrease both buffalo activity during darting and the immobilization time, reducing the risks of both direct and delayed capture mortality.

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Table 1. Model-selection results for *a priori* post capture survival models of K parameters. Survival (\emptyset) is modeled as a function of *year* (*yr*), *season* (*seas*), *age* (*a*), *sex* (*s*), *bTB status* (*tb*), *capture* (*c*), *capture-lag* (*clag*), *capture method* (*cmet*), *number of immobilizations* (*i*), *drought period* (*d*) and *drought-lag* (*dlag*). Plus signs between parameters indicate additive effects and asterisks signify interactions. Included for each model is the sample size corrected Akaike Information Criterion (AICc), the difference in AICc between each model and the model with the lowest AICc (Δ AICc), the likelihood of each model (L) and the Akaike weight (w_i) for each model. Models are ranked in decreasing level of support of being the best model (w_i).

	Model	K	AICc	Δ AICc	L	w_i
1	$\emptyset\{a+s+(a*s) +seas+c+(seas*c)\}$	11	372.20	0.00	1.00	0.38
2	$\emptyset\{a+s+(a*s) +seas+cmet\}$	11	372.58	0.38	0.82	0.31
3	$\emptyset\{a+s+(a*s) +seas+c\}$	10	375.57	3.38	0.18	0.07
4	$\emptyset\{a+s+(a*s) +seas+c+(c*s)\}$	11	375.88	3.68	0.16	0.06
5	$\emptyset\{a+s+(a*s) +seas+c+tb\}$	11	376.54	4.34	0.11	0.04
6	$\emptyset\{a+s+(a*s) +seas+dlag\}$	11	377.14	4.94	0.08	0.03
7	$\emptyset\{a+s+(a*s) +seas+d\}$	11	377.22	5.03	0.08	0.03
8	$\emptyset\{a+s+(a*s) +seas+clag\}$	10	377.33	5.14	0.08	0.03
9	$\emptyset\{a+s+(a*s) +seas\}$	9	378.94	6.74	0.03	0.01
10	$\emptyset\{a+s+(a*s) +seas+yr+c\}$	14	379.17	6.98	0.03	0.01
11	$\emptyset\{a+s+(a*s) +seas+tb\}$	10	379.59	7.39	0.02	0.01
12	$\emptyset\{a+s+(a*s) +seas+tb+(seas*tb)\}$	11	380.77	8.58	0.01	0.01
13	$\emptyset\{a+s+(a*s) +seas+c+i\}$	13	380.96	8.76	0.01	0.00
14	$\emptyset\{a+s+seas\}$	6	381.27	9.08	0.01	0.00
15	$\emptyset\{a+s+(a*s) +seas+yr+tb\}$	14	382.28	10.09	0.01	0.00
16	$\emptyset\{a+s+(a*s)\}$	8	383.39	11.19	0.00	0.00
17	$\emptyset\{a+s+seas (a*s)+(a*seas)+(s*seas)\}$	13	383.45	11.26	0.00	0.00
18	$\emptyset\{a+s+(a*s) +(seas*yr)\}$	12	388.80	16.60	0.00	0.00

Table 2. Model averaged parameter estimates of variables affecting survival probability of radiocollared buffalo. Numeric values indicate the level of the parameter. Reference classes are 2001, wet season, no drought, no capture related variable, females, age 1-3 and bTB negative. Lower 95% confidence intervals (LCI) and upper 95% confidence intervals (UCI) are used to evaluate the strength of evidence of parameter estimates. Only parameter estimates of interest is presented.

Model	Estimate	S.E.	LCI	UCI
<i>season1</i>	0.69	0.40	-0.10	1.47
<i>capture1</i>	0.18	0.51	-0.82	1.17
<i>age2</i>	-1.48	1.10	-3.63	0.68
<i>age3</i>	-0.08	0.64	-1.34	1.17
<i>age4</i>	0.84	0.56	-0.26	1.94
<i>sex1</i>	0.76	0.60	-0.41	1.92
<i>captlag1</i>	-0.67	0.66	-1.97	0.63
<i>captmethod2</i>	0.35	0.37	-0.37	1.08
<i>captmethod3</i>	1.70	1.32	-0.90	4.29
<i>drought1</i>	-0.21	0.22	-0.64	0.21
<i>drought-lag1</i>	0.29	0.29	-0.29	0.86
<i>imm2</i>	-0.22	0.22	-0.65	0.21
<i>imm3</i>	-0.24	0.24	-0.72	0.23
<i>imm4</i>	-0.37	0.37	-1.09	0.36
<i>season*capture</i>	1.56	1.24	-0.86	3.99

Table 3. Model-selection results for *a priori* female reproduction models of K parameters. Calving rate (δ) is modeled as a function of the *year of reproduction* (yr), *female age* (a), *month of capture* (c), *the number of immobilizations* (i), and *the female's herd* (h). Plus signs indicate additive effects and asterisks between parameters signify interactions. Included for each model is the sample size corrected Akaike Information Criterion (AICc), the difference in AICc between each model and the model with the lowest AICc (Δ AICc), the likelihood of each model (L) and the Akaike weight (w_i) for each model. Models are ranked in decreasing level of support of being the best model (w_i).

Model	K	AICc	Δ AICc	L	w_i
(1) $\delta\{yr + a + c\}$	11	439.87	0.00	1.00	0.58
(2) $\delta\{yr + c\}$	9	441.34	1.47	0.48	0.28
(3) $\delta\{yr\}$	5	445.21	5.34	0.07	0.04
(4) $\delta\{yr + a\}$	7	445.35	5.48	0.06	0.04
(5) $\delta\{yr + a + i\}$	10	445.56	5.69	0.06	0.03
(6) $\delta\{yr + a + h + i + c\}$	15	446.60	6.74	0.03	0.02
(7) $\delta\{yr + a + h\}$	8	447.32	7.45	0.02	0.01
(8) $\delta\{yr + a + (y*a) + c\}$	19	454.44	14.57	0.00	0.00
(9) $\delta\{yr + a + (y*a)\}$	15	459.47	19.60	0.00	0.00

Table 4. Model averaged *a priori* model parameter estimates of variables affecting calving rates of radiocollared buffalo. Reference classes are 2005, age 12+, never captured before reproduction, and the Lower Sabie herd. Numeric values indicate the level of the parameter. Lower 95% confidence intervals (LCI) and upper 95% confidence intervals (UCI) are used to evaluate the strength of evidence of parameter estimates. Only parameter estimates of interest is presented, and parameters in bold have 95% CI not overlapping zero.

Parameter	Estimate	S.E.	LCI	UCI
<i>year1</i>	0.76	0.47	-0.16	1.68
<i>year2</i>	0.28	0.41	-0.53	1.09
<i>year3</i>	-1.65	0.50	-2.63	-0.67
<i>year4</i>	0.14	0.35	-0.55	0.83
<i>age1</i>	-0.76	0.49	-1.72	0.20
<i>age2</i>	-0.30	0.34	-0.96	0.36
<i>c1</i>	1.61	0.65	0.33	2.89
<i>c2</i>	1.02	0.49	0.06	1.97
<i>c3</i>	0.50	0.44	-0.36	1.36
<i>c4</i>	0.73	0.49	-0.23	1.68
<i>imm1</i>	0.15	0.19	-0.23	0.52
<i>imm2</i>	0.44	0.47	-0.49	1.37
<i>imm3</i>	0.26	0.30	-0.33	0.86

Table 5. Model-selection results after the addition of four *a posteriori* models to the calving rate model set. Calving rate (δ) is modeled as a function of the *year of reproduction (yr)*, *female age (a)*, *month of capture (c)*, *the number of immobilizations (i)*, *the female's herd (h)*, *drought (d)* and *drought-lag (dlag)*. K is the number of parameters in a model. Plus signs indicate additive effects and asterisks between parameters indicate interactions. Included for each model is the sample size corrected Akaike Information Criterion (AICc), the difference in AICc between each model and the model with the lowest AICc (Δ AICc), the likelihood of each model (L) and the Akaike weight (w_i) for each model. Models are ranked in decreasing level of support of being the best model (w_i).

Model	K	AICc	Δ AICc	L	w_i
(1) $\delta\{dlag+a+c\}$	8	436.90	0.00	1.00	0.63
(2) $\delta\{yr + a + c\}$	11	439.87	2.96	0.23	0.14
(3) $\delta\{dlag\}$	1	440.21	3.30	0.19	0.12
(4) $\delta\{yr + c\}$	9	441.34	4.43	0.11	0.07
(5) $\delta\{yr\}$	5	445.21	8.31	0.02	0.01
(6) $\delta\{yr + a\}$	7	445.35	8.44	0.01	0.01
(7) $\delta\{yr + a + i\}$	10	445.56	8.65	0.01	0.01
(8) $\delta\{yr + a + c + i + h\}$	15	446.60	9.70	0.01	0.00
(9) $\delta\{yr + a + h\}$	8	447.32	10.41	0.01	0.00
(10) $\delta\{yr + a + (y*a) + c\}$	19	454.44	17.53	0.00	0.00
(11) $\delta\{yr + a + (y*a)\}$	15	459.47	22.57	0.00	0.00
(12) $\delta\{d+a+c\}$	8	463.86	26.96	0.00	0.00
(13) $\delta\{d\}$	1	470.25	33.35	0.00	0.00

Table 6. Model averaged post hoc parameter estimates of variables affecting calving rates of radiocollared buffalo. All *a posteriori* models were used in computing averaged parameter and standard error estimates. Reference classes are 2005, age 12+, never captured before reproduction, and the Lower Sabie herd. Numeric values indicate the level of the parameter. Lower 95% confidence intervals (LCI) and upper 95% confidence intervals (UCI) are used to evaluate the strength of evidence of parameter estimates. Only parameter estimates of interest is presented, and parameters in bold have 95% CI not overlapping zero.

Parameter	Estimate	S.E.	LCI	UCI
<i>year1</i>	0.76	0.69	-0.59	2.12
<i>year2</i>	0.28	0.31	-0.33	0.89
<i>year3</i>	-1.65	1.37	-4.33	1.03
<i>year4</i>	0.14	0.19	-0.24	0.52
<i>age1</i>	-0.76	0.44	-1.62	0.10
<i>age2</i>	-0.30	0.33	-0.95	0.36
<i>c1</i>	1.50	0.65	0.23	2.78
<i>c2</i>	0.80	0.43	-0.04	1.64
<i>c3</i>	0.40	0.42	-0.42	1.22
<i>c4</i>	0.44	0.41	-0.36	1.24
<i>imm1</i>	0.15	0.16	-0.16	0.46
<i>mmi2</i>	0.44	0.45	-0.44	1.33
<i>imm3</i>	0.26	0.27	-0.27	0.80
<i>drought</i>	-0.31	0.31	-0.91	0.30
<i>drought-lag</i>	1.90	0.79	0.35	3.45

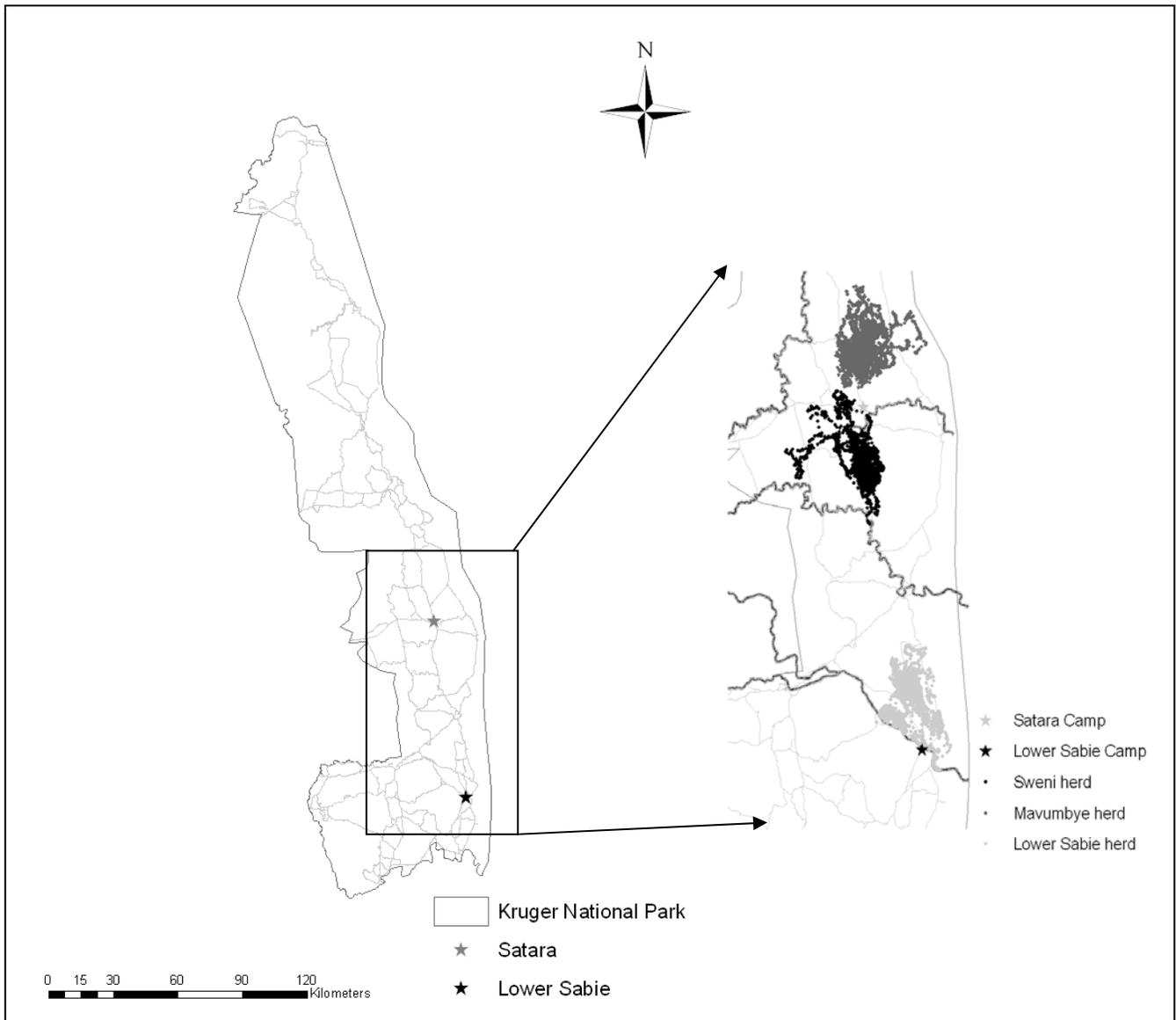


Figure 1. A total of 881 buffalo captures or recaptures were made in Kruger National Park during the Buffalo TB Project. GPS point positions from three radiocollars indicate the approximate home ranges of two herds (Mavumbye and Sweni) north and south of Satara, while the Lower-Sabie herd ranges further south.

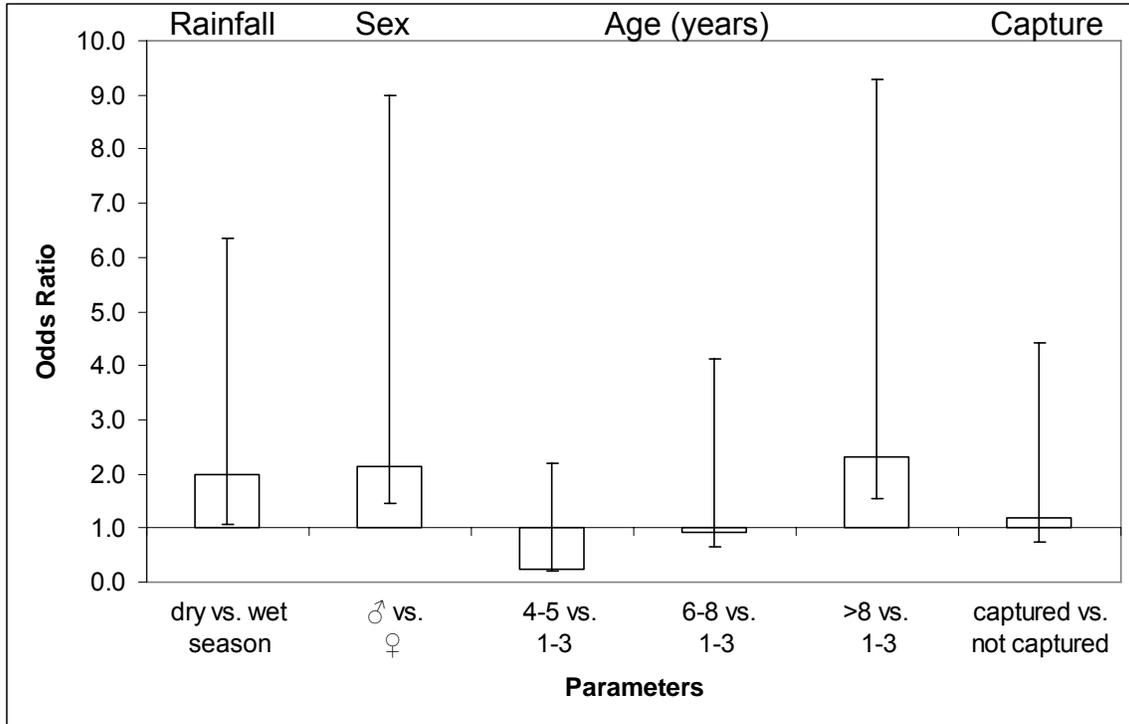


Figure. 2. The relative odds of death (\pm 95% CI) calculated for key survival variables. The odds of death double during dry seasons opposed to wet seasons, for males vs. females and animals older than 8 years compared to juveniles age 1-3. Captures only increase the odds of death to 1.16. Capture odds ratio 95% CI overlap one, reducing support capture as a principle factor influencing mortality

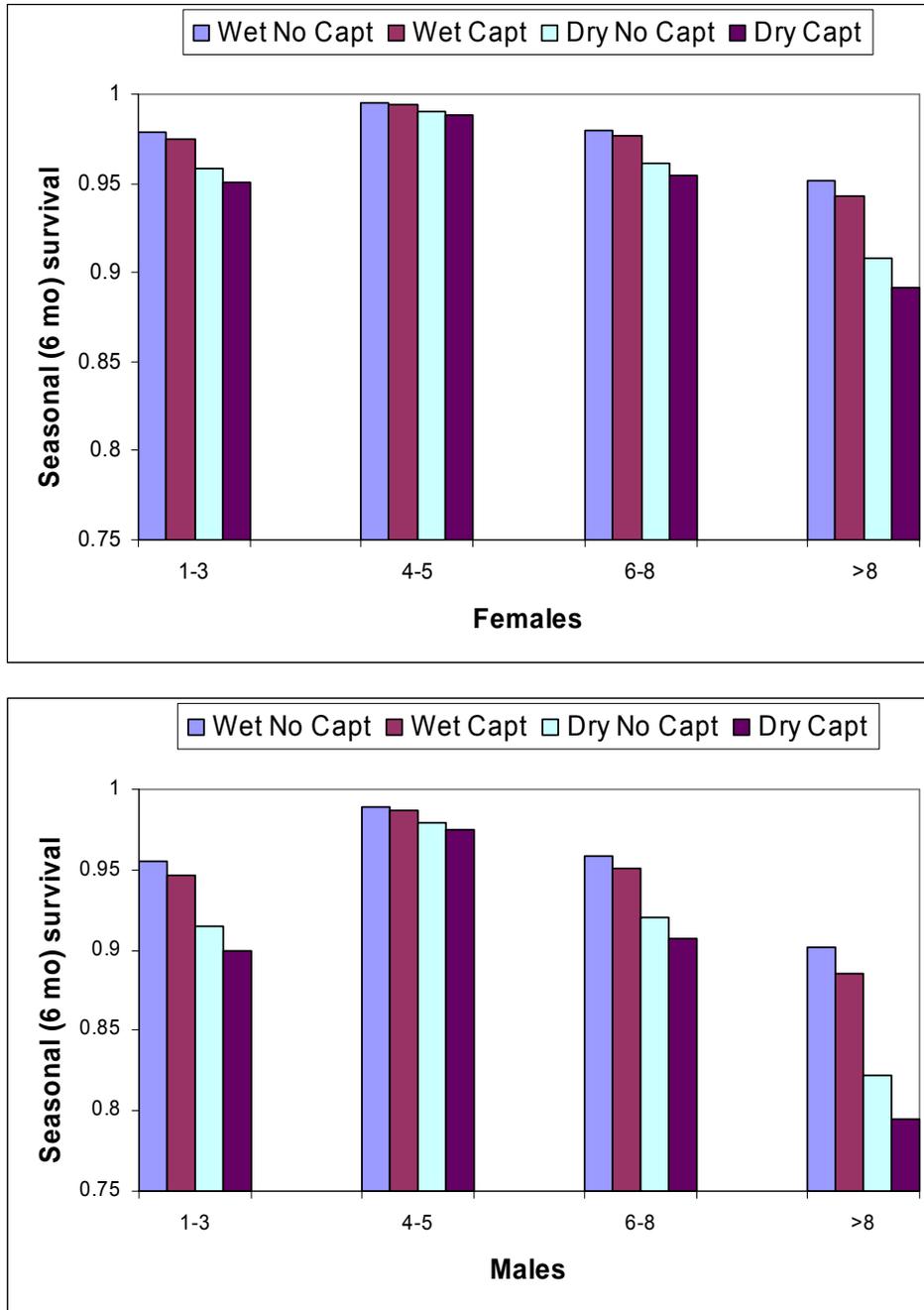


Figure. 3. Comparative six month seasonal survival estimates for male and female buffalo of different age categories (1-3, 4-5, 6-8 and >8 years), corrected for each season and capture history (captured or not captured in last three months). Survival estimates are based on averaged parameter estimates over all *a priori* models. Constant hazard is assumed over the seasonal interval. Survival rates of captured buffalo are decreased, but less important than the influence of sex, age and season.

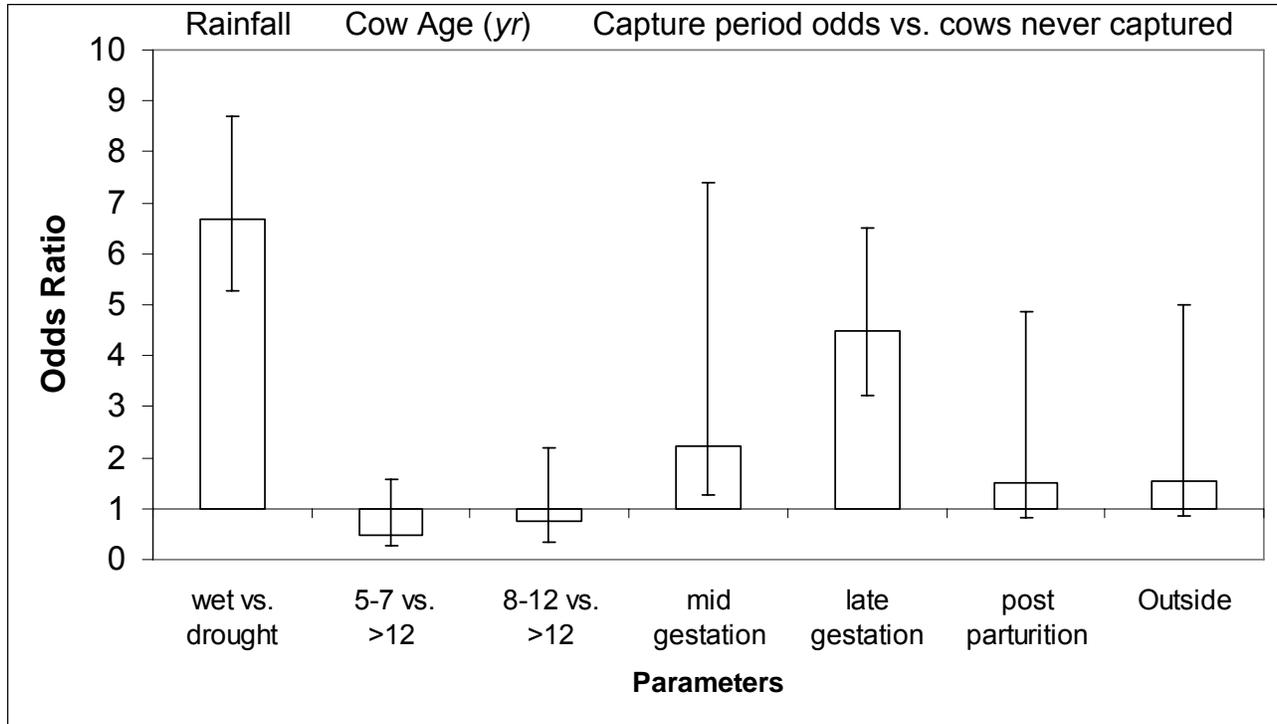


Figure 4. The relative odds of calving (\pm 95% CI) of important determinants of calving rate, as predicted by model selection. The odds of calving is >6 times higher when rainfall is good during the conception phase relative to drought years. All captured classes (cow captured in mid gestation, late gestation, post parturition, or outside the current reproductive cycle) have higher probability of calving compared to control cows never captured. Cows older than 12 years have higher calving rates. The upper confidence levels for season (31.45) and late gestation captures (16.04) odds ratios are not drawn to scale.

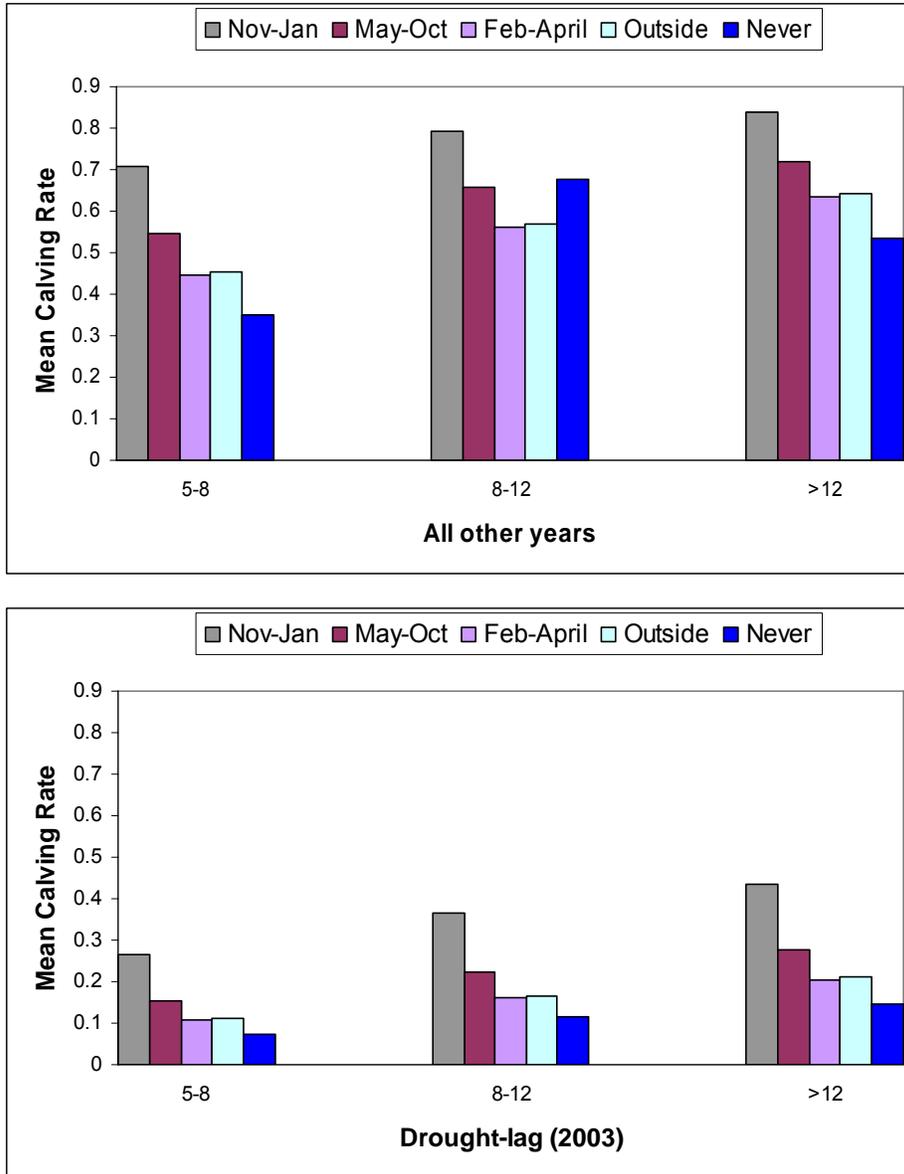


Figure 5. Comparative calving rates for buffalo cows in different rainfall periods, age and capture classes, as predicted by post hoc model parameter coefficients. Five capture classes is presented, and indicate when the last capture was made (late gestation, mid gestation, post parturition, outside the current reproductive cycle, or the female was never captured). Calving rate show the greatest response to decrease in rainfall in the conception period.