

## ECOLOGICAL-ECONOMIC MODELS OF SUSTAINABLE HARVEST FOR AN ENDANGERED BUT EXOTIC MEGAHERBIVORE IN NORTHERN AUSTRALIA

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**ABSTRACT.** How can one manage wildlife under a suite of competing values? In isolation, the ecological economics of native wildlife harvest, threatened species conservation and control of exotic species are all well established sub-disciplines of wildlife management. However, the wild banteng (*Bos javanicus*) population of northern Australia represents an interesting combination of these aspirations. A native bovid of Southeast Asia now 'endangered' in its native range, banteng were introduced into northern Australia in 1849. Today, a population of 8,000–10,000 resides on one small, isolated peninsula in western Arnhem Land, Northern Territory and is harvested by both recreational (trophy) and aboriginal subsistence hunters. Indigenous, industry and conservationist stakeholders differ in their requirements for population management. Here we analyze the ecological and economic costs/benefits of a series of potential harvest management options for Australia's banteng population, with the aim being either to: (1) maximize sustainable yield (MSY); (2) maximize harvest of trophy males; (3) maximize indigenous off-take; (4) suppress density or completely eradicate the population; (5) minimize risk of extinction whilst limiting range expansion; (6) scenarios incorporating two or more of options 1–5. The modeling framework employed stochastic, density-regulated matrix population models with life-history parameters derived from (i) allometric relationships (for estimating  $r_{\max}$ , generation length, fecundity and densities for a banteng-sized mammal) and (ii) measured

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vital rates for wild and captive banteng and other *Bos* spp. For each management option, we present a simple economic analysis that incorporates estimated costs of management implementation and associated profits projected. Results demonstrate that revenue of >AU\$200,000 is possible from meat production and safari hunting without compromising long-term population stability or the conservation status of this endangered bovid.

**KEY WORDS:** Aboriginal, banteng, economics, harvest, hunting, Leslie matrix, safari, stochasticity, sustenance, sustainability, viability.

**Introduction.** The drive to reconcile the development of strong economies without further compromising ecosystem ‘health’ (*sensu* Leopold [1949]) is problematical due to the conflict in the mechanisms and politics underlying their separate goals (Coleman [1996], Buckingham [1998], Rapport [1998], Lackey [2001], Song and M’Gonigle [2001], Ullsten and Rapport [2001]). This conflict is epitomized in the struggle to curtail the global species extinction crisis (Ceballos and Ehrlich [2002], Thomas et al. [2004]) while maintaining sustainable rates of wildlife harvest (Munasinghe [1994], Brashares et al. [2001], Jerozolinski and Peres [2003]). Recent attempts to quantify ecosystem services and natural capital within an economic framework have provided some points of consilience (Costanza et al. [1997], Wilson [1998]), although it is still unclear in many specific situations how best to manage both conservation and economic values of wildlife species simultaneously.

In isolation, the ecological socioeconomics of native wildlife harvest, e.g., Berkes et al. [1994], Barrett and Arcese [1998], Rodriguez [2000], Bodmer and Lozano [2001], Haule et al. [2002], the conservation of threatened species (Tracy and Brussard [1996], Morris and Doak [2002]), and the eradication of exotics (Wilman [1996], Rainbolt and Coblenz [1997], Sharov and Liebhold [1998], Myers et al. [2000], Forsyth et al. [2004]), are all well established sub-disciplines of wildlife management. However, there are situations where the different aspirations of these sub-disciplines compete. The most familiar of these is the often vexed relationship between wildlife conservation and harvest, even though most threatened species harvested by humans are managed with the view to reduce or eradicate the threatening process itself, i.e., the harvest, (Noss [1998], Li et al. [2000], Newing [2001], Norris [2004]).

One of the most exceptional combinations of these competing wildlife management aspirations is found in the far north of Australia, where an introduced non-native ungulate, the banteng (*Bos javanicus*), has proliferated on one small (22,000 ha), semi-isolated peninsula. Approximately 20 individuals were introduced in 1849 during the earliest phase of European settlement (Calaby [1975]) and today the population numbers approximately 8,000–10,000 (K. Saalfeld, unpubl. data). The area where this population resides is both a National Park and aboriginal land, and is co-managed by a combined government-aboriginal council (Foster [1997]). Individuals are harvested occasionally by aboriginal land owners (deKoninck [2005]), and a limited number of trophy males are permitted to be shot by recreational safari hunters each year for which a royalty is paid to the traditional aboriginal owners (Choquenot [1993], deKoninck [2005]). There are no data available on the level of illegal harvest, although this appears to be extremely low given the peninsular isolation of the National Park and strictly controlled permitting of all non-aboriginals visiting the region.

Outside Australia, wild banteng exist today only in small, isolated herds in south-eastern Asia (Hedges [1996]) and are consequently listed as ‘Endangered’ under IUCN Red List criteria (IUCN [2000]). Until recently, the population in northern Australia was usually assumed to be comprised of hybrids of domestic or other *Bos* species. However, recent genetic analysis has demonstrated that Australian banteng are indeed pure-strain *Bos javanicus* and therefore represent the largest population of this endangered species in the world (Bradshaw et al. [2006]).

Because aboriginal, government and conservationist stakeholders differ in their requirements for population management, our aim is to provide a series of options that marry different management outcomes. To this end, we developed alternative stochastic, density-regulated matrix population models with life-history parameters derived from (i) allometric relationships and (ii) measured vital rates for wild and captive banteng and other *Bos* spp. The different management options presented include (1) maximizing sustainable yield (MSY) for meat production, (2) maximizing harvest of trophy males, (3) indigenous sustenance harvest, (4) partial or complete eradication such as has been the goal for other exotic species in Australian national parks (Ridpath and Waithman [1988], Brook et al. [2006]), (5) minimizing risk of extinction,

and (6) scenarios incorporating two or more of options 1–5. Finally, for each management option we present a simple economic analysis that incorporates estimated costs of implementation and projected profits.

**Methods: Banteng life history.** Like other *Bos* species, banteng are a relatively long-lived ungulate that may exceed 15 years (G. Kirby, pers. comm.), and Choquenot [1993] reported a maximum age of 17 years from a shot sample of banteng in Australia. Male banteng are considered to have a relatively higher survival rate than other congeners (Kirby [1979]); therefore, we assumed equal longevity for the sexes. Adult and foetal sex ratios are near 1:1 (Choquenot [1993]). Survival is generally high during adult years, i.e.,  $> 0.95$ , given the relatively lower investment in milk production by females to other *Bos* sp. (Kirby [1979]), but is reduced in the first year or two of life, followed by a peak around the age of 2–3 years (Choquenot [1993]). Fertility is characterized by high conception rates ( $> 95\%$ ), delayed maturity (3–5 years) and a gradual reduction in reproductive output after the age of seven years (Kirby [1979], Choquenot [1993]). Sexually dimorphic banteng also demonstrate reduced growth relative to other *Bos* species, with males reaching maximum size ( $\sim 600$  kg) at 5–6 years, and females ( $\sim 300$  kg) at 3–4 years (Kirby [1979], Choquenot [1993]).

**Base parameters.** To derive age-specific survival rates and smooth sampling variation, we fitted a 3-parameter exponential rise function to the data of Choquenot [1993], of the form:

$$\hat{s}_x = a_s \cdot e^{(b_s/x+c_s)}$$

where  $a_s$ ,  $b_s$  and  $c_s$  are constants. Similarly, age-specific fertility rates were derived by fitting a 3-parameter log-normal distribution to the data, of the form:

$$\hat{m}_x = a_m \cdot e^{[-0.5(\log_e(x/x_0)/b_m)^2]}$$

again, where  $a_m$ ,  $b_m$  and  $x_0$  are constants.

**Modeling environment.** Our modeling approach was to begin with a deterministic, density-independent Leslie matrix population model (Leslie [1945]) that describes the average demography of the banteng population. We defined a 17-year age-classified model for both sexes combined based on the maximum age of females reported by Choquenot [1993]. Here, the resultant  $34 \times 34$  matrix contains the female survival and fecundity values in the upper left quadrant, the production of males in the lower left quadrant and the survival of males in the lower right quadrant. The upper right quadrant only contains zeros (Akçakaya [1998]). Although the use of a two-sex model in this case is identical to a female age-classified model given the equality in sex ratio and longevity assumed between the sexes, the format was necessary to model specific sex-biased harvest regimes, see details below. The matrix entries themselves were derived assuming a birth-pulse, pre-breeding design, with first-year survival incorporated into the fertility coefficients (Caswell [2001]). For the deterministic matrix, the dominant eigenvalue ( $\lambda_1$ ) indicates the rate of population change through time (Leslie [1945], Caswell [2001]). We then examined progressively more complex modeling scenarios that incorporated stochastic and regulatory effects. Unless otherwise indicated, all projection intervals were set to 30 years, and, for all stochastic simulations, the number of iterations was set to 1000.

**Somatic growth.** We assumed a constant growth function for each sex based on measured cross-sectional morphometric data (Choquenot [1993]), following the von Bertalanffy growth function (von Bertalanffy [1938]):

$$M_x = M_{\max} - (M_{\max} - M_0) \cdot e^{-kx}$$

where  $M_x$  is predicted mass at age  $x$ ,  $M_{\max}$  is the maximum mass attainable,  $M_0$  is birth weight,  $x$  is age in years and  $k$  is the rate constant (expressed in  $\text{year}^{-1}$  units). Using female  $M_{\max} = 300$ , male  $M_{\max} = 600$ ,  $M_0 = 17$  (Choquenot [1993]) and, assuming maturity at 4 and 6 years for females and males, respectively, we estimated  $k_{\text{female}} = 0.4732$  and  $k_{\text{male}} = 0.3385$ .

**Density dependence.** The density-dependent processes in large mammals generally occur within survival and fertility rates (Messier and Crête [1984], Freeland and Choquenot [1990]), but large reductions in either parameter tend to occur only as the population approaches carrying capacity,  $K$  (Fowler [1981]). We examined whether the current estimate of population density was likely to represent  $K$ . The latest population estimate is between 8,000 and 10,000 individuals within an area of 2200 km<sup>2</sup> (K. Saalfeld, unpubl. data). This translates into an observed density of 4.09 animals/km<sup>-2</sup> (9000 / 2200 km<sup>-2</sup>), which is well above the density reported for wild Javan *B. javanicus* (Hoogerwerf [1970], Freeland [1990]), but consistent with the observation that feral herbivores in Australia can achieve densities many times greater than those observed in native populations (Freeland and Choquenot [1990]). We also calculated the theoretical population density for mammalian herbivores based on body size using the relationship described by Damuth [1981] and modified by Freeland [1990]:

$$\log_{10} \text{Density} = 4.196 - 0.74 \cdot (\log_{10} W)$$

where Density is expressed in animals per km<sup>2</sup> and  $W$  = body mass in grams. Average body mass for all individuals was taken as the average of maximum male and female body mass described in the growth function (450,000 g), which gives a predicted density = 1.01 banteng/km<sup>2</sup>. Thus, we are confident that the high densities observed for Australian banteng represent maximum or near-maximum densities for this species.

We constructed three separate density-dependent functions for (1) survival of neonates to age 1 ( $s_0$ ), (2) survival of individuals  $\geq 1$  year ( $s_{1+}$ ), and (3) fertility ( $m$ ) using a flexible 4-parameter logistic expression of the form:

$$\text{parameter} [s_0, s_{1+}, m] = z_{dd} + \frac{a_{dd}}{1 + (N/c_{dd})^{b_{dd}}}$$

to modify the  $s_0$ ,  $s_{1+}$  and  $m$  'parameters.' Here,  $N$  is population size and  $z_{dd}$ ,  $a_{dd}$ ,  $b_{dd}$  and  $c_{dd}$  are constants. Because of the log-normal distribution of  $m$  described above, we adjusted the log-normal coefficient  $a_m$  as a logistic function of population size to produce a maximum  $m$  at the lowest population size.

Maximum and minimum values of  $s_0$ ,  $s_{1+}$  and  $m$  were set to vary between population sizes thought to represent initial population size and carrying capacity ( $K$ ), respectively (here, maximum survival occurs at minimum population density.  $K$  was assumed to equal the mean current population estimate of 9,000, and initial population size was set to 20 individuals. For this exercise, the bounds of the survival and reproductive rates were set according to one of two criteria:

(1) the measured vital rates from the early 1990's, which were assumed to represent those taken from a population at or near  $K$  (Choquenot [1993]). Thus, minimum  $s_{1+}$  was set to 0.92 according to the fitted exponential rise function described above. This value was also used to set maximum  $s_0$  based on the observation that survival during the first year of life is generally low in this species (Kirby [1979], Choquenot [1993]). Minimum  $s_0$  was set to a value that resulted in the density-independent matrix projection producing a stable population size over the projection interval (0.62). Minimum  $a_m$  used to predict  $m_x$  in the log-linear function was also set to the value estimated from measured vital rates (Choquenot [1993]);

(2) maximum vital rates were taken from both measured and theoretical values where maximum  $s_{1+}$  was set to near-guaranteed survival (0.99). Maximum  $a_m$  was set to a value that resulted in the  $m_7$  for prime females of the *Bos* genus estimated from allometric relationships (Peters [1983]):

$$m_{\max} = \frac{12000 \cdot M^{-0.73}}{2}$$

where  $M$  is the mass prediction (in g) for seven-year old females derived from the von Bertalanffy growth function. In this case,  $M$  was set to 289,000 g; therefore,  $m_{\max} = 0.62$ .

**Environmental stochasticity.** Megaherbivores are affected both by the abundance and timing of rains that modify the absolute quantity and quality of browse and graze (Caughley and Gunn [1993], Oosterheld et al. [1998], Harrington et al. [1999], Moss and Croft [1999], Georgiadis et al. [2003]). Banteng in Australia are subject to a wide range of moisture extremes given the position of the Cobourg Peninsula in a wet-dry tropical system. Choquenot [1993] measured the long-term coefficient of variation in rainfall for the peninsula at 24 percent. We used this value to construct a survival multiplier that would reduce

average survival in low-rainfall years and increase average survival in above-average rainfall years. We standardized the calculation of a rainfall standard deviation ( $sd_1$ ) using the coefficient of variation and mean = 1. We then calculated a uniform random multiplier drawn from a sample bounded by  $1 - 2 \cdot sd_1$  and  $1 + 2 \cdot sd_1$  to provide a stochastic modification to all survival rates per time step, using the justification that variation in rainfall would cause variation in survival (as observed for feral buffalo, Boulton and Freeland [1991]). The resultant samples of corrected survival were bounded by the minimum and maximum survival rates described for density dependence.

**Extreme environmental perturbations (catastrophes).** In addition to the variance in survival rate modified by the application of a rainfall multiplier for environmental stochasticity, we also modeled the probability and severity of extreme environmental perturbations (also known as ‘catastrophes’) because their occurrence can have a major impact on the probability of extinction (Young [1994], Reed et al. [2003]). Given the lack of data on the occurrence and severity of catastrophes for banteng in the Cobourg Peninsula, we chose to model the theoretical relationship between generation length and catastrophe occurrence for vertebrates as estimated by Reed et al. [2003]. For this we estimated the probability of catastrophe occurrence as:

$$Pr(\text{catastrophe}) = \frac{0.147}{\bar{A}}$$

where  $\bar{A}$  is mean generation time (Reed et al. [2003]). There are several methods for calculating  $\bar{A}$ , but for the purposes of this calculation we took  $\bar{A}$  = the mean age of parents of the offspring produced by a population at the stable age distribution (Caswell [2001]). In all projections a catastrophe was implemented at time step  $t$  when a random uniform number bounded by 0 and 1 was  $\leq Pr(\text{catastrophe})$ . To model the severity of a catastrophe once invoked, we used the power function:

$$Y = 2510 \cdot 0.9376^x$$

where  $Y$  = the probability that any given catastrophe will have a severity of  $x$  (Reed et al. [2003]). We constructed this equation for



probabilities ranging from 0 to 1 and solved for  $x$ . Then, we produced a random uniform number between 0 and  $Y_{\max}$  to predict the severity of the catastrophe once invoked.

**Demographic stochasticity.** The variation in vital rates increases as populations become small, so that extinction risk can actually increase even when vital rates remain constant or increase (Akçakaya [1991], [1998]). To account for this statistical variation in vital rates as a function of population size, we resampled survival rates using the binomial distribution where the new survival rates in time step  $t + 1$  were the binomially resampled number of surviving individuals per age class divided by the total number of individuals in time step  $t$ . Similarly, the modified fecundity vector was the Poisson resampled number of offspring produced per age class (as a function of the number of reproductive females).

**Tertiary sex ratio.** The decline in population growth rate when a population is small is known as the Allee effect (Legendre et al. [1999], Stephens et al. [1999]), and this may result from the reduced probability of finding a suitable partner with which to mate when the tertiary sex ratio, i.e., the ratio of the rarer sex to the total number of breeding adults, is low (Stephens et al. [1999], Stephens and Sutherland [1999]). For large polygynous ungulates, the normal tertiary sex ratio is approximately 0.83 females to males (Bessa-Gomes et al. [2004]). Therefore, highly skewed female-bias in the tertiary sex ratio is expected for banteng, given their polygynous mating system. However, in harvest scenarios where adult males were removed systematically from the population, we hypothesize that there is an upper threshold beyond which the probability that a female will be mated and subsequently reproduce is compromised (induced Allee effect). This is especially probable for Australian banteng given that movements of adult males are low between different regions of the Cobourg Peninsula (Bradshaw, unpubl. data). Therefore, in all harvest scenarios modeled in the present study we set the maximum tertiary sex ratio to 0.95 and beyond which all female fecundity = 0.

**Economic analysis.** The economics of observed and predicted banteng harvest were divided into three main income categories: (1) revenue derived from the commercial sale of banteng beef through the current Australian beef-trade market, (2) replacement value of meat derived from harvested banteng (aboriginal use), and (3) revenue derived from royalties paid to the aboriginal management board by safari hunting organizations for each trophy animal shot. Basic functions to modify production costs and limit the number of banteng bulls for which royalties could be received from the safari industry were also provided for the commercial sale of beef and safari hunting categories, respectively.

Potential revenue generated from the sale of banteng beef was based on the Eastern Young Cattle Indicator (EYCI) which is a seven-day rolling average of 24 young cattle categories from 26 saleyards across Queensland, New South Wales and Victoria, Australia. The EYCI is expressed as a value per kg dressed meat in Australian dollars and is a good indicator of market prices (Meat and Livestock Australia [2003]). Product sourced from more remote areas result in price fluctuation that is certainly influenced by other price trends such as distance from major markets, focus on other trades groups, e.g., live export, local buyer factors, abattoir availability, and regional weather variation (Meat and Livestock Australia [2003]). For our simulations we accessed the historical EYCI values from 1996–2004 and expressed them in 2004 AU\$. We calculated mean annual EYCI because all projections occurred in one-year increments. We then calculated the first-order auto-correlation between  $EYCI_{t+1}$  and  $EYCI_t$  and used this to predict the mean EYCI for a given time step. Here,  $EYCI_t$  was drawn from a random Gaussian distribution with mean = 1st-order auto-correlated EYCI and variance = total variance in mean EYCI among years.

To predict the total amount of saleable meat, we estimated the dressed weight of carcasses of harvested animals according to the von Bertalanffy growth functions for each sex (see above) and the dressing proportion measured for captive banteng = 0.526 (Kirby [1979]). Each ‘total harvest rate’ was distributed uniformly over the adult age classes to which it pertained (adult females > 2 years; adult males > 3 years; trophy bulls > 5 years), then the number of individuals within each age class were translated into a total live mass by the growth functions. The sum of all harvested live mass multiplied by the dressing proportion

gave the total amount of marketable banteng beef for each harvest scenario.

Trophy-sized male banteng are currently hunted via two safari hunting operations within the national park boundaries. An annual quota of 30 males is set by the management board, although insufficient demand for safari hunting often prevents filling the entire quota during certain years (P. Whitehead, pers. comm.). To this end, we established a hypothetical function where the probability of sequestering sufficient demand to fulfill the annual quota reduces logarithmically as a function of the quota (Meat and Livestock Australia [2003]). Safari hunting clients currently spend  $\sim$  AU\$10,000 for a single hunt, i.e., one adult male permitted to be shot per tag purchased, of which approximately 25 percent is paid to the aboriginal management board as royalties. For the purposes of this analysis, we assumed that after 40 animals were shot the demand for additional safari hunts would decline dramatically (P. Whitehead, pers. comm.). This translates into the logarithmic function:

$$h_{\text{safari}} = h_{\text{max}} \cdot (1 - d^n)$$

where  $h_{\text{safari}}$  is the number of mature males for which full royalties are paid, i.e., the number of males shot per year for which royalties are received,  $h_{\text{max}}$  is the ‘maximum’ demand for full-fee paying safari hunters (40),  $d$  was set to 0.97 arbitrarily so that the curve of the demand probability increased logarithmically with an increasing number of trophy tags purchased, i.e.,  $d$  sets the curvature of the function, and  $n$  is the possible range of safari tags issued. In this instance, we assumed that the safari price of AU\$10,000 remained unchanged from year to year, that all issued tags result in a kill, and full royalties per mature male shot = AU\$2,500. We defined a mature male as one  $\geq$  6 years of age. The function essentially limits the number of harvested trophy males that provide full royalties in any given year based on the input values, even if culling rates, e.g., for density reduction purposes, exceed the number of safari tags sold.

Meat production costs were based on interviews with A. Trier (Project Mgr., Northern Territory Indigenous Pastoral Project, Katherine, Northern Territory, Australia). Although costs vary widely from region to region, transport and mustering costs in remote bush areas are thought to be approximately AU\$150 per head (price includes helicopter and vehicle muster, truck/barge transport to abattoir, etc.)

for established cattle farming operations. Rather than assume a constant cost per individual killed, we constructed a hypothetical cost-modifier function where the difficulty in hunting individuals successfully increases non-linearly as the total population is reduced, see also Boulton and Freeland [1991]. We chose a simple exponential decay function of the form:

$$\text{cost} = y_0 + ae^{-bN}$$

where  $N$  is the total banteng population size and  $y_0$ ,  $a$  and  $b$  are constants estimated at 113.07, 534.9 and  $3.3 \times 10^{-4}$ , respectively. This function was set arbitrarily to vary between a maximum cost per head of AU\$500 at low population densities to \$150 per head near or at carrying capacity (analogous to a type II functional response from predator-prey systems, see Holling [1959]). Costs were capped at these minimum and maximum values accordingly. There were no costs assumed for safari royalties apart from the cap on royalties received each year.

**Results: Somatic growth.** The maximum likelihood fits of the von Bertalanffy growth functions indicated rate constants of  $0.472 \text{ year}^{-1}$  and  $0.339 \text{ year}^{-1}$  for females and males, respectively. To put this into context, Moran ([1973]) reported a growth rate of 0.22 kg/day for 22- to 37-month old banteng steers. Our function predicted an average male growth rate of 0.28 kg/day during the same interval. The difference is likely due to the inclusion of a reduced growth period during the drier (winter) months in Morans ([1973]) study.

**Deterministic base matrix.** The survival function derived from Choquenot ([1993]) was

$$\hat{s}_x = 0.0582 \cdot e^{(0.2511/x + 0.1678)}$$

where  $x$  is the age in years, and the fertility function became:

$$\hat{m}_x = 0.4468 \cdot e^{[-0.5 \cdot (\log_e(x/6.1960)/0.3533)]^2}.$$

The deterministic, density-independent base matrix derived from the above age-specific vital rates produced a dominant eigenvalue  $\lambda_1 = 1.0229$  ( $r = 0.0227$ ) so that the end population was approximately 1.4 times larger than the 1990 population after 15 years. This supports

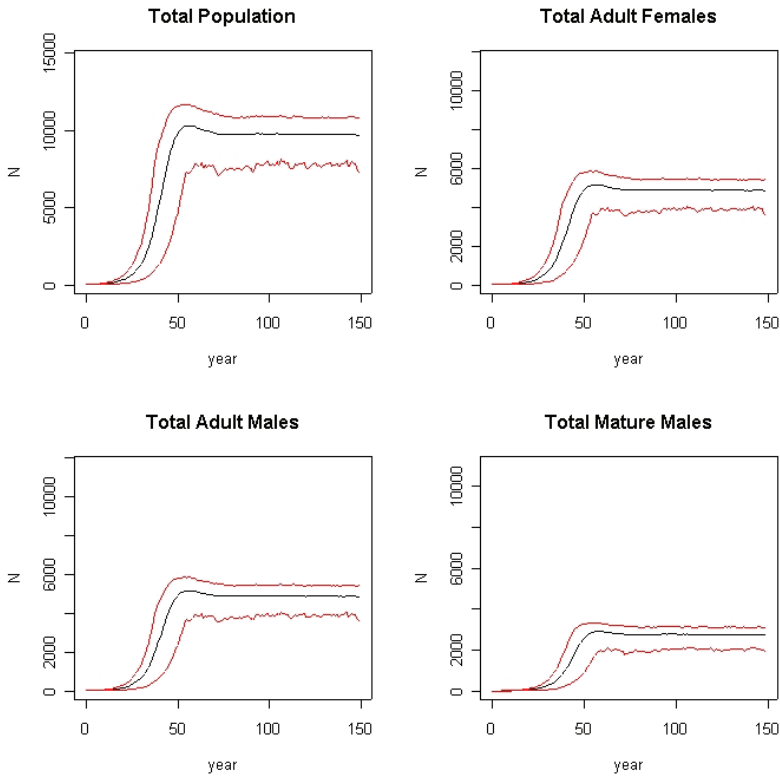


FIGURE 1. Projected population of banteng from a founder population of 20 individuals over 150 years since establishment. Carrying capacity is set at 9,000, and all projections incorporate demographic and environmental stochasticity in addition to catastrophic mortality events. No human hunting mortality was incorporated.

the view that the population has increased since the early 1990's (Choquenot [1993], K. Saalfeld, unpubl. data). The net reproductive rate ( $R_0$  is the expected production of daughters by a female during her lifetime, Caswell [2001]) was 1.20. Mean generation time ( $\bar{A}$  is the time required for the population to increase by a factor of  $R_0$ , Caswell [2001]) was 7.94 years, and the mean age of the parents of the offspring produced by a population at the stable age distribution was 7.02 years.

**Stochastic density-dependent projection without kills.** Based on an initial population size of 20, i.e., the number of banteng introduced in 1849, and 1000 simulations, the simulated population reached stability approximately 70 years post-introduction and varied between 7,500 and 11,000 thereafter, Figure 1. This scenario predicts that the population achieves  $K$  approximately 2 times faster than what was assumed to have occurred in the national park. However, it should be noted that unquantified sporadic killing of individuals for control and scientific purposes, meat and safari hunting have occurred over the 150 years since introduction and were not included in this projection.

*Scenario 1. Maximum sustainable yield.* For this scenario we assumed that all revenue was derived solely from the harvest of adult animals (females  $> 2$  years and males  $> 3$  years) for the production and sale of banteng beef. No revenue from safari hunting was considered. The lower 95 percent confidence interval of minimum population size after a 30-year projection declined rapidly after approximately 450 animals killed per annum, which translated into a profit range of approximately AU\$197,000–313,500/year, Figure 2. Profit is defined as the total revenue minus the production costs, but does not include other costs such as administrative costs of running the program. To avoid the higher rates of population extinction at this harvest rate, we consider the effects of harvesting  $\sim 250$  animals/year: that harvest rate resulted in a mean minimum population size after 30 years of 4300–8100 (47–90 %  $K$ ), and a total profit of approximately AU\$110,000–171,000, Figures 2a, b. The marked decrease in total meat production and profit at higher harvest levels (700 killed/year) indicates the higher probability of driving the population to extinction and the increased costs of lowered hunting efficiency at low population density.

*Scenario 2. Maximum harvest of trophy males.* For this scenario we assumed that all revenue was derived solely from safari royalties (hunting males  $\geq 6$  years of age). Given the cap on royalties receivable each year, the optimal number of mature male banteng to harvest was 80 per year, giving a total maximum profit of approximately AU\$91,000 per year, Figure 3a. Of course, this value would increase if the cap on royalties receivable function was altered to increase the number of marketable safari tags purchased by safari clients. Although harvest

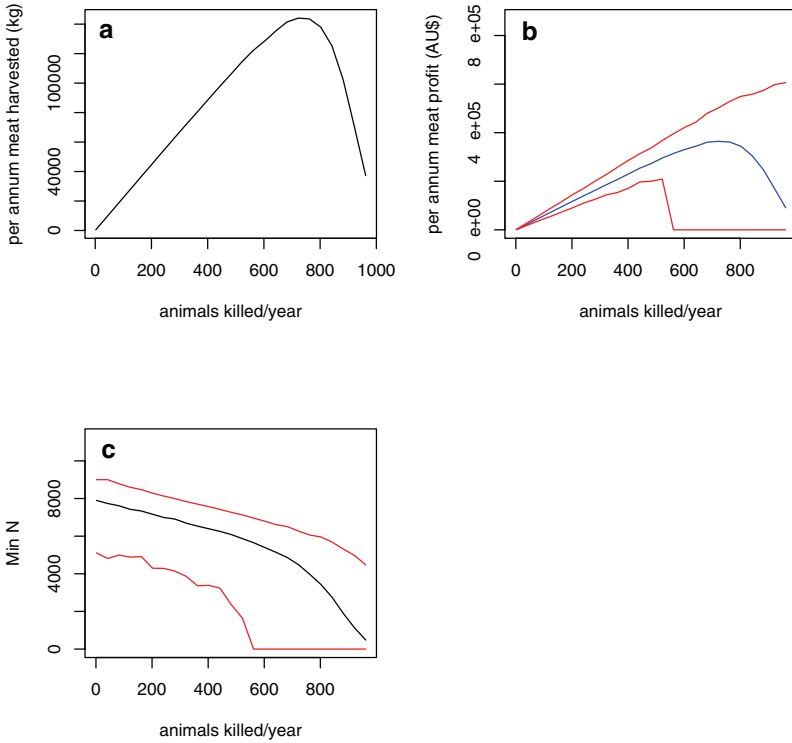


FIGURE 2. (a) Estimated quantity of marketable meat derived from incrementing levels of adult harvest over a 30-year projection interval; (b) corresponding predicted annual profit (AU\$) based on fluctuating market values for beef (with upper and lower 95 percent confidence limits); (c) minimum population size realized during the 30-year projection for each level of annual adult harvest (with upper and lower 95 percent confidence limits).

of mature males did not reduce total population size to unacceptable levels, i.e., population crash, until  $> 600$  individuals per year, Figure 3b, approximately 360 mature males killed per year resulted in complete eradication of this class at the lower 95 percent confidence level, Figure 3c.

*Scenario 3. Indigenous harvest.* Although the incidence of aboriginal subsistence harvest of banteng to supplement protein intake appears to be relatively low in the national park (deKoninck [2005]), we modeled

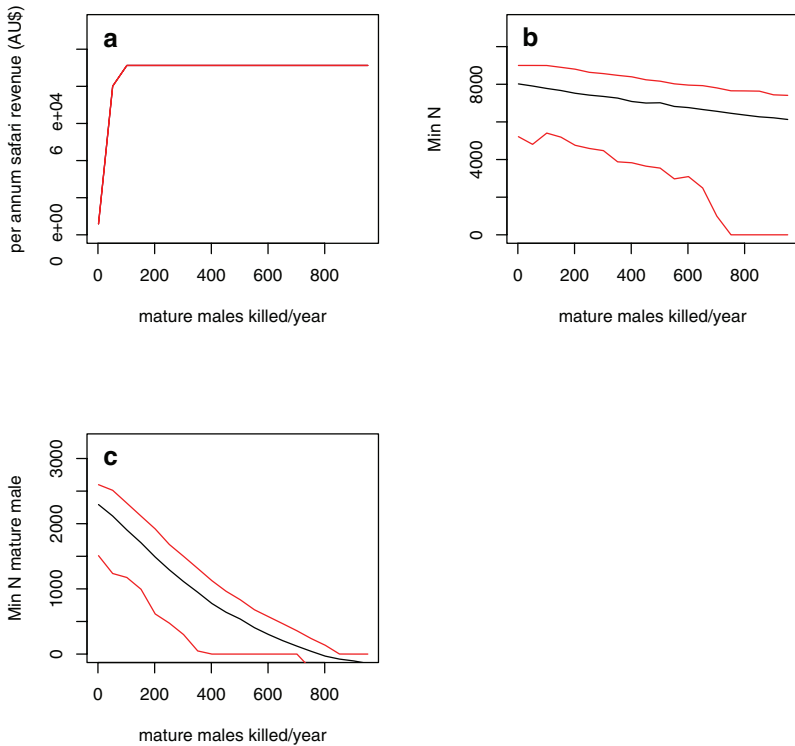


FIGURE 3. (a) Estimated annual profit derived from mature male banteng (> 5 years) safari hunting royalties over the 30-year projection interval; (b) minimum population size realized during the 30-year projection for each level of annual harvest of mature males (with upper and lower 95 percent confidence limits); (c) minimum population size of remaining mature males during the 30-year projection for each level of annual harvest of mature males (with upper and lower 95 percent confidence limits).

the replacement value of banteng beef if the entire aboriginal population within the region of Cobourg Peninsula used banteng as their major source of protein. The total aboriginal population within the district of Minjilang and Outstations (includes Cobourg Peninsula, Croker Island and the northwest corner of Arnhem Land) in 2001 was 254 persons, of which 36 percent were over the age of 14 (Australian Bureau of Statistics [2001]). Assuming the average Australian adult consumes 67 g/day red meat, and children consume approximately half this



value (Dieticians Association of Australia [2004]), the total maximum indigenous consumption of banteng beef would be 5087 kg/year.

Harvesting adults indiscriminately with respect to age would achieve an equivalent mass of meat at approximately 16 animals/year, Figure 4a. Assuming a 'shop bought' replacement cost of AU\$10/kg consumed (T. Griffiths, pers. comm.), this translates to a total replacement value of approximately AU\$50,000 per annum, Figure 4b. At this level of harvest, and even twice the number of adults harvested, the minimum population size is approximately stable over the 30-year projection, Figure 4c. However, this analysis does not take human population growth into account and may underestimate replacement value over several decades.

*Scenario 4. Density reduction or eradication.* For this scenario we modeled the kill rate required to reduce the population to some desired lower proportion of the current population size. For this we used a projection interval of 5 years and estimated the number of adults (females > 2 years and males > 3 years) that would have to be killed per year to reduce the population to desired levels. The projection interval of 5 years was used to portray a realistic management scheme within a fundable time-frame. Results show that by targeting only adults, a reduction of the initial population of 9000 individuals by 50 percent is achieved by culling approximately 750–1400 individuals per year for the 5-year program, Figure 5. To achieve higher reductions in population size require progressively higher rates of annual cull due to the survival of juveniles during the 5-year projection and the reduction in hunting efficiency (Boulton and Freeland [1991], Figure 5).

*Scenario 5. Minimum viable population size (MVP).* Intensive and prolonged harvest regimes could conceivably lead to population reductions to a point where random environmental and demographic stochasticity could result in the extinction of the remaining population. However, the increase in vital rates at low population densities (density dependence) used in the previous models necessarily results in an increasing population when  $N$  is low. Therefore, we chose instead to assess the probability that a founder population of banteng would succumb to quasi-extinction, i.e., reduction to a set threshold number of individuals, Otway et al. [2004], given normal variation in environ-

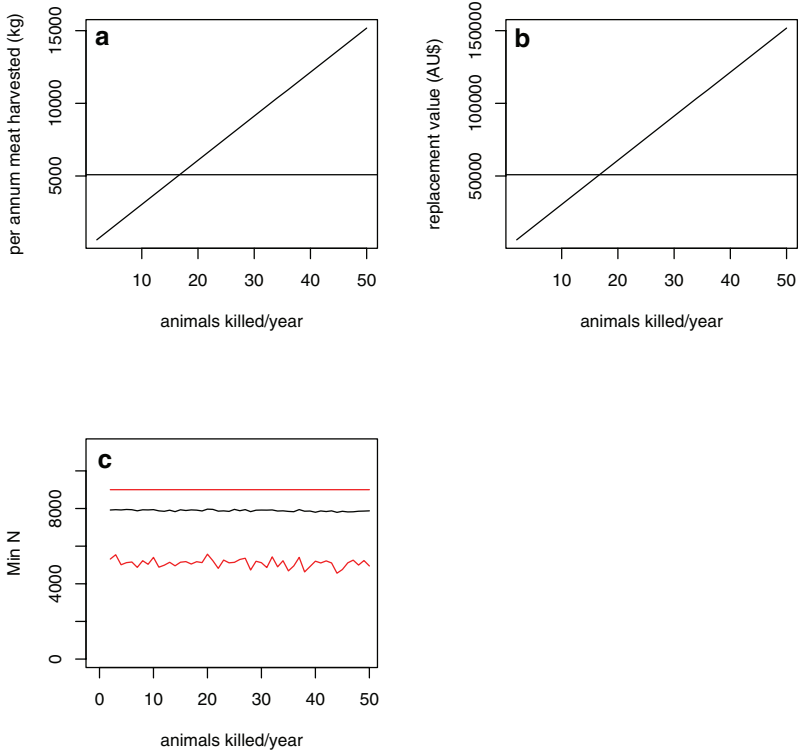


FIGURE 4. (a) Estimated quantity of aboriginal sustenance meat derived from incrementing levels of adult harvest over a 30-year projection interval; also shown is the estimated required quantity of banteng meat required to support an aboriginal population of approximately 250 persons (Australian Bureau of Statistics [2001]) for one year, i.e., 5087 kg; (b) corresponding total predicted replacement value of the sustenance harvest assuming a replacement value of AU\$10/kg banteng beef; (c) minimum population size realized during the 30-year projection for each level of annual adult sustenance harvest (with upper and lower 95 percent confidence limits).

mental (rainfall) and demographic rates. For this scenario we modeled ‘founder’ populations ranging from 20 to 200 individuals distributed randomly between the sexes and among the adult age classes. We ran 1000 projections over 100 years for each starting vector and estimated the probability that the projected population would decrease below 20 individuals at any point during the projection (quasi-extinction). The results demonstrate that, with an entirely random sample of adults,

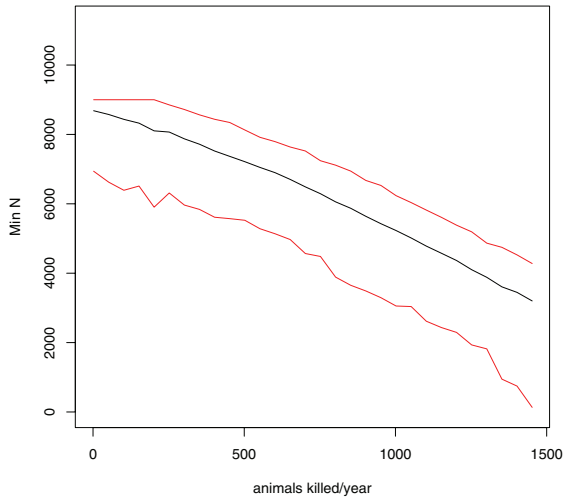


FIGURE 5. Estimated range of required annual kill rates to reduce the population to targeted minimum sizes over a five-year culling program.

probability of quasi-extinction is  $< 5\%$  at an initial size of approximately 40 individuals, Figure 6a.

A second MVP model was run where density dependence relationships for fecundity and survival were removed. This is because under the density-dependent scenario above, the increase in vital rates at low population sizes necessarily reduces the risk of extinction due to chance events (Ginzburg et al. [1990]). Therefore, we used a start matrix producing long-term stability, see above, and modified the matrix entries for environmental (rainfall and catastrophe) and demographic stochasticity only (density independent vital rates). In this case, we considered the population to be extinct if the population dropped below 2 individuals at any time during the 100-year projection. Under this scenario, the probability of extinction was also reduced to about 5 percent with an initial population of 40 individuals, Figure 6b.

*Scenario 6. Combining meat production, safari hunting and population reduction.* The lower 95 percent confidence interval of minimum population size after a 30-year projection declined rapidly after approximately 300 animals killed per annum, which translated into a to-

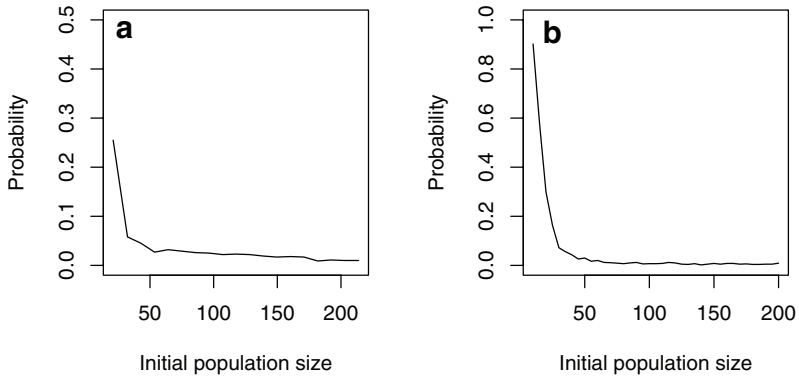


FIGURE 6. (a) Probability of quasi-extinction, i.e., population drops below 20 individuals during a 100-year projection, for incrementing founder population sizes. Here, the founder population is distributed randomly between the sexes and age classes and survival and fecundity are density dependent; (b) probability of quasi-extinction, i.e., population drops below 2 individuals during a 100-year projection, assuming no density dependence and a founder population distributed among the sex and age classes according to the stable stage distribution.

tal profit range of approximately AU\$224,000–306,000/year, of which a maximum of AU\$91,000 per year was derived from safari revenue, Figure 7. Harvesting  $\sim 250$  animals/year resulted in a total profit of approximately AU\$200,000–272,000 and results in a reduction of the population to 37–90 %  $K$ , Figure 7.

**Discussion.** The aims of this paper were to provide potential ecological and economic outcomes of specific management strategies for the Australian population of banteng. We have demonstrated that achieving a balance between population exploitation and control, economic gain and conservation management of the endangered herd of banteng of northern Australia is a realistic proposition. Nevertheless, we did not set out to provide unequivocal advice regarding the particular choice of management scenarios to implement, because that decision depends on many political and socioeconomic aspects that could not be modeled explicitly (Brook et al. [2006]). Neither did we model the tourist value of banteng within Garig Gunak Barlu National Park, given that infor-

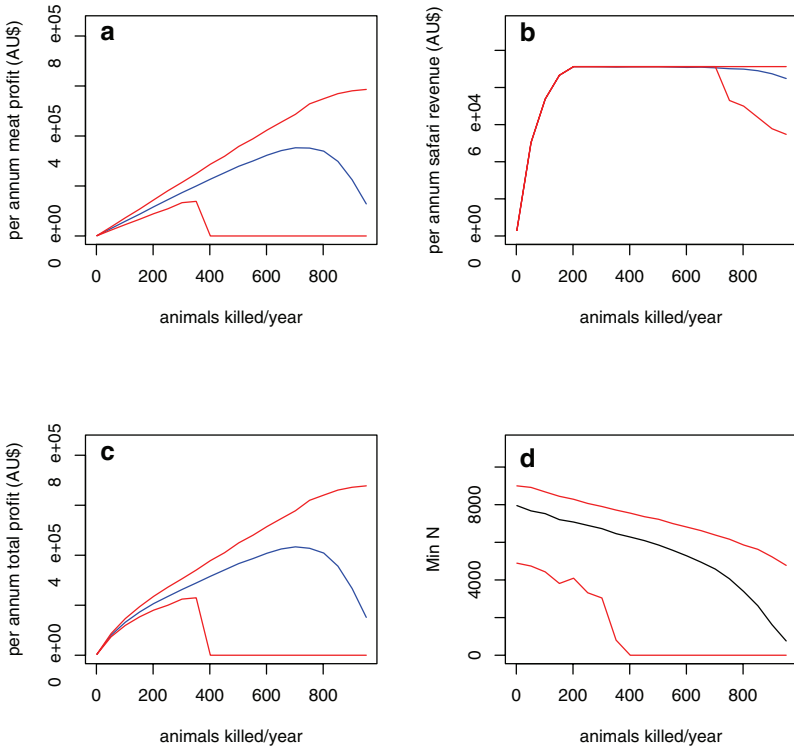


FIGURE 7. (a) Estimated annual profit for commercial meat production in a general adult harvest over a 30-year projection interval for incrementing levels of annual kill rates (with upper and lower 95 percent confidence limits); (b) estimated annual safari profit derived from the mature male (> 5 years) component of the annual kill (with upper and lower 95 percent confidence limits); (c) total annual profit combining revenue from commercial meat production and safari royalties (with upper and lower 95 percent confidence limits); (d) minimum population size realized during the 30-year projection for each level of annual adult harvest (with upper and lower 95 percent confidence limits).

mation in this regard is currently unavailable. Additionally, the recent determination of Australian banteng as genetically pure *Bos javanicus* raises many issues regarding the role of Australian authorities in conserving endangered species outside of their native ranges (Bradshaw et al. [2006], Brook et al. [2006]). Thus, all harvest scenarios modeled

are only indicative of potential returns in light of political management decisions for this species (Brook et al. [2006]).

Our analysis of harvest potential has revealed that even at apparently high rates of annual culling, the long lifespan of this tropical bovid ensures that the population remains relatively stable over projection intervals of 30 years. Of course, the ability to translate these harvests into tangible economic returns depends on many factors not necessarily considered in our analysis; however, our approach has indicated that there is significant potential to achieve annual returns in excess of AU\$200,000 with the combination of profits derived from meat production and safari hunting. We attempted to incorporate realistic scenarios of harvest and economic return despite the assumptions made regarding demand, production costs and market values. However, we were unable to provide a detailed economic analysis for the costs associated with establishing a meat-production industry, e.g., stockyard fencing, etc., for banteng in this remote region of Arnhem Land, so estimates of the potential annual returns do not reflect these costs. Revenue derived from safari hunting therefore appears to be one of the most efficient and least detrimental forms of harvest at this time (Wilkie and Carpenter [1999]).

Our risk analyses suggest that this species is fairly robust in the face of extensive harvest rates and low population sizes, including the potential for short-term catastrophic declines due, for instance, to a disease epidemic or severe drought. The success of the original 20 animals released into the wild in the mid-19th century, i.e., total current population is 8,000–10,000, is a testament to this capacity. Additionally, our estimates of extinction risk at small initial population sizes support the general conclusion that a founder population of 20–40 animals stands a high probability ( $> 95\%$ ) of increasing to carrying capacity within relatively short time frames, e.g., 60 years, if undisturbed by excessive hunting pressure. This is expected based on observations that large-bodied animals, being well buffered against short-term environmental variation due to their long life-spans and more opportunistic reproductive strategies, seem to be better colonizers (Pimm et al. [1988]) or have better translocation success (Griffith et al. [1989]) than smaller species, and herbivores tend to be better colonizers than carnivores (Griffith et al. [1989]). Indeed, it has been shown for long-lived birds that approximately 30 individuals are required for their

successful establishment in new or historically occupied areas (Legendre et al. [1999]).

It should also be noted that the genetic implications of harvest scenarios were not considered here. Despite the apparent robustness of this species to extensive culling, the reduction of genetic variation with excessive harvest rates may lead to inbreeding depression that can cause reductions in survival probability and reproductive output, and thus increase the probability of extinction at low population sizes (Crnokrak and Roff [1999], Frankham et al. [2002], Spielman et al. [2004]). Sex-biased harvest regimes like those posed here for trophy males can also result in an overall reduction in genetic diversity. For example, the targeting of large-horned rams in bighorn sheep (*Ovis canadensis*) by trophy hunters can lead to reduced genetic diversity in the population because these rams tend to have higher-than-average heterozygosity (Fitzsimmons et al. [1995]). Perhaps a more serious short-term concern is the reduction in size of highly heritable traits such as horns and body weight with sustained harvest of trophy males (Coltman et al. [2003]), a form of artificial 'selection' against these characteristics. Thus, although the overall rates of harvest as modeled in this paper may indicate a high propensity for resilience, possibly more conservative harvest rates than proposed are advisable to avoid the potential negative impacts on genetic diversity.

In conclusion, the marriage of different management goals such as conservation, aboriginal subsistence and substantial economic returns appears possible for the wild banteng population of northern Australia. Despite the observation that little overt damage to native flora and fauna within the region has occurred since the introduction of banteng over 150 years ago (Bowman and Panton [1991]), a reduction in population size to reduce potential impacts and maintain indigenous and commercial utilization is an approach that can be harmonious with the long-term persistence of endangered banteng in the wild. With the caveat that more research is required to determine the genetic diversity of this particular population and its potential resilience to sustained rates of harvest, the culling regimes proposed are compatible with increased revenue to aboriginal and non-aboriginal park custodians without compromising the conservation or tourist value of this species.

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## REFERENCES

- H.R. Akçakaya [1991], *A Method for Simulating Demographic Stochasticity*, *Ecol. Model.* **54**, 133–136.
- H.R. Akçakaya [1998], *RAMAS Metapop: Viability Analysis for Stage-Structured Metapopulations* (version 3.0), Applied Biomathematics, Setauket, NY.
- Australian Bureau of Statistics [2001], *Australian Indigenous Geographical Classification Maps and Census Profiles*, 2001; ABS Cat. No. 4706.0.30.001. Commonwealth of Australia, Canberra.
- C.B. Barrett and P. Arcese [1998], *Wildlife Harvest in Integrated Conservation and Development Projects: Linking Harvest to Household Demand, Agricultural Production, and Environmental Shocks in the Serengeti*, *Land Econ.* **74**, 449–465.
- F. Berkes, P.J. George, R.J. Preston, A. Hughes, J. Turner and B.D. Cummins [1994], *Wildlife Harvesting and Sustainable Regional Native Economy in the Hudson and James Bay Lowland, Ontario*, *Arctic* **47**, 350–360.
- C. Bessa-Gomes, S. Legendre and J. Clobert [2004], *Allee Effects, Mating Systems and the Extinction Risk in Populations with Two Sexes*, *Ecol. Lett.* **7**, 802–812.
- R.E. Bodmer and E.P. Lozano [2001], *Rural Development and Sustainable Wildlife Use in Peru*, *Conserv. Biol.* **15**, 1163–1170.
- W.J. Boulton and W.J. Freeland [1991], *Models for the Control of Feral Water Buffalo (Bubalus bubalis) Using Constant Levels of Offtake and Effort*, *Wildlife Research* **18**, 63–73.
- D.M.J.S. Bowman and W.J. Panton [1991], *Sign and Habitat Impact of Banteng (Bos javanicus) and Pig (Sus scrofa)*, *Cobourg Peninsula, Northern Australia*, *Austral. J. Ecol.* **16**, 15–17.
- C.J.A. Bradshaw, Y. Isagi, S. Kaneko, D.M.J.S. Bowman and B.W. Brook [2006], *Conservation Value of Non-Native Banteng in Northern Australia*, *Conserv. Biol.* **20**, 1306–1311.



J.S. Brashares, P. Arcese and M.K. Sam [2001], *Human Demography and Reserve Size Predict Wildlife Extinction in West Africa*, Proc. Royal Soc. London, Biol. Sci. **268**, 2473–2478.

B.W. Brook, D.M.J.S. Bowman, C.J.A. Bradshaw, B.M. Campbell and P.J. Whitehead [2006], *Managing an Endangered Asian Bovid in an Australian National Park: The Role and Limitations of Ecological-Economic Models in Decision-Making*, Environ. Manage. **38**, 463–469.

D.E. Buckingham [1998], *Does the World Trade Organization Care about Ecosystem Health—The Case of Trade in Agricultural Products*, Ecosyst. Health **4**, 92–108.

J.H. Calaby [1975], *Introduction of Bali Cattle to Northern Australia*, Austral. Vet. J. **51**, 108.

H. Caswell [2001], *Matrix Population Models: Construction, Analysis, and Interpretation*, Sinauer Assoc., Inc., Sunderland, MA, USA.

G. Caughley and A. Gunn [1993], *Dynamics of Large Herbivores in Deserts: Kangaroos and Caribou*, Oikos **67**, 47–55.

G. Ceballos and P.R. Ehrlich [2002], *Mammal Population Losses and the Extinction Crisis*, Science **296**, 904–907.

D. Choquenot [1993], *Growth, Body Condition and Demography of Wild Banteng (Bos javanicus) on Cobourg Peninsula, Northern Australia*, J. Zool. **231**, 533–542.

W.G. Coleman [1996], *Biodiversity and Industry Ecosystem Management*, Environ. Manage. **20**, 815–825.

D.W. Coltman, P. O'Donoghue, J.T. Jorgenson, J.T. Hogg, C. Strobeck and M. Festa-Bianchet [2003], *Undesirable Evolutionary Consequences of Trophy Hunting*, Nature **426**, 655–658.

R. Costanza, R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raksin, P. Sutton and M. van den Belt [1997], *The Value of the World's Ecosystem Services and Natural Capital*, Nature **387**, 253–260.

P. Crnokrak and D.A. Roff [1999], *Inbreeding Depression in the Wild*, Heredity **83**, 260–270.

J. Damuth [1981], *Population Density and Body Size in Mammals*, Nature **290**, 699–700.

V. deKoninck [2005], *Joint Management of Banteng (Bos javanicus) in a Contested Cultural Landscape: Observations and Implications*, Human Dimen. Wildlife **10**, 123–135.

Dieticians Association of Australia [2004], *Red Meat*, Dieticians Association of Australia. Available from <http://www.dsa.asn.au>.

N.N. Fitzsimmons, S.W. Buskirk and M.H. Smith [1995], *Population History, Genetic Variability, and Horn Growth in Bighorn Sheep*, Conserv. Biol. **9**, 314–323.

D.M. Forsyth, R.P. Duncan, M. Bomford and G. Moore [2004], *Climatic Suitability, Life-History Traits, Introduction Effort, and the Establishment and Spread of Introduced Mammals in Australia*, Conserv. Biol. **18**, 557–569.

D. Foster [1997], *Gurig National Park: The First Ten Years of Joint Management*, Austral. Institute of Aboriginal and Torres Strait Islander Studies, Canberra.

C.W. Fowler [1981], *Density Dependence as Related to Life History Strategy*, *Ecol.* **62**, 602–610.

R. Frankham, J.D. Ballou and D.A. Briscoe [2002], *Introduction to Conservation Genetics*, Cambridge Univ. Press, Cambridge, U.K.

W.J. Freeland [1990], *Large Herbivorous Mammals: Exotic Species in Northern Australia*, *J. Biogeog.* **17**, 445–449.

W.J. Freeland and D. Choquenot [1990], *Determinants of Herbivore Carrying Capacity: Plants, Nutrients, and Equus asinus in Northern Australia*, *Ecol.* **71**, 589–597.

N. Georgiadis, M. Hack and K. Turpin [2003], *The Influence of Rainfall on Zebra Population Dynamics: Implications for Management*, *J. Appl. Ecol.* **40**, 125–136.

L.R. Ginzburg, S. Ferson and H.R. Akçakaya [1990], *Reconstructability of Density Dependence and the Conservative Estimate of Extinction Risk*, *Conserv. Biol.* **4**, 63–70.

B. Griffith, J.M. Scott, J.W. Carpenter and C. Reed [1989], *Translocation as a Species Conservation Tool: Status and Strategy*, *Science* **245**, 477–480.

R. Harrington, N. Owen-Smith, P.C. Viljoen, H.C. Biggs, D.R. Mason and P. Funston [1999], *Establishing the Causes of the Roan Antelope Decline in the Kruger National Park, South Africa*, *Biol. Conserv.* **90**, 69–78.

K.S. Haule, F.H. Johnsen and S.L.S. Maganga [2002], *Striving for Sustainable Wildlife Management: The Case of Kilombero Game Controlled Area, Tanzania*, *J. Environ. Manage.* **66**, 31–42.

S. Hedges [1996], *Proposal for Inclusion of Banteng (Bos javanicus) in CITES Appendix I*, pp. IUCN/SSC Asian Wild Cattle Specialist Group, IUCN/SSC Wildlife Trade Programme, Thai Government, Bangkok.

C.S. Holling [1959], *Some Characteristics of Simple Types of Predation and Parasitism*, *Canad. Entomol.* **91**, 385–398.

A. Hoogerwerf [1970], *Udung Kulon: The Land of the Last Javan Rhinoceros*, Brill, Leiden.

IUCN [2000], *The IUCN Red List of Threatened Species*, IUCN, Gland, Switzerland.

A. Jerzolimski and C.A. Peres [2003], *Bringing Home the Biggest Bacon: A Cross-Site Analysis of the Structure of Hunter-Kill Profiles in Neotropical Forests*, *Biol. Conserv.* **111**, 415–425.

G.W.M. Kirby [1979], *Bali Cattle in Australia*, *FAO World Animal Review* **31**, 1–7.

R.T. Lackey [2001], *Values, Policy, and Ecosystem Health*, *Biosci.* **51**, 437–443.

S. Legendre, J. Clobert, A.P. Møller and G. Sorci [1999], *Demographic Stochasticity and Social Mating System in the Process of Extinction of Small Populations: The Case of Passerines Introduced to New Zealand*, *The Amer. Naturalist* **153**, 449–463.

A. Leopold [1949], *A Sand County Almanac*, Ballantine Books, New York.

P.H. Leslie [1945], *On the Uses of Matrices in Certain Population Mathematics*, *Biometrika* **33**, 183–212.

- Y.M. Li, Z.X. Gao, X.H. Li, S. Wang and J. Niemela [2000], *Illegal Wildlife Trade in the Himalayan Region of China*, Biodivers. Conserv. **9**, 901–918.
- Meat and Livestock Australia [2003], *Eastern Young Cattle Indicator*, Meat and Livestock Australia/Sydney Futures Exchange. Available from: <http://www.mla.com.au>
- F. Messier and M. Crête [1984], *Body Condition and Population Regulation by Food Resources in Moose*, Oecologia **65**, 44–50.
- J.B. Moran [1973], *Liveweight Changes of Braham Cross, Shorthorn, Banteng and Buffalo Steers Grazing Improved Pastures at Darwin, N.T.*, J. Austral. Institute Agr. Sci. **39**, 68–70.
- W.F. Morris and D.F. Doak [2002], *Quantitative Conservation Biology*, Sinauer Assoc. Inc., Sunderland, MA, USA.
- G.L. Moss and D.B. Croft [1999], *Body Condition of the Red Kangaroo (Macropus rufus) in Arid Australia: The Effect of Environmental Condition, Sex and Reproduction*, Austral. J. Ecol. **24**, 97–109.
- M. Munasinghe [1994], *Economic and Policy Issues in Natural Habitats and Protected Areas*, in *Protected Area Economics and Policy: Linking Conservation and Sustainable Development* (M. Munasinghe and J. McNeely, eds.), World Bank, Washington, DC, pp. 15–49.
- J.H. Myers, D. Simberloff, A.M. Kuris and J.R. Carey [2000], *Eradication Revisited: Dealing with Exotic Species*, Trends Ecol. Evol. **15**, 316–320.
- H. Newing [2001], *Bushmeat Hunting and Management: Implications of Duiker Ecology and Interspecific Competition*, Biodivers. Conserv. **10**, 99–118.
- K. Norris [2004], *Managing Threatened Species: The Ecological Toolbox, Evolutionary Theory and Declining-Population Paradigm*, J. Appl. Ecol. **41**, 413–426.
- A.J. Noss [1998], *The Impacts of Baaka Net Hunting on Rainforest Wildlife*, Biol. Conserv. **86**, 161–167.
- M. Oesterheld, C.M. Dibella and H. Kerdiles [1998], *Relation between NOAA-AVHRR Satellite Data and Stocking Rate of Rangelands*, Ecol. Appl. **8**, 207–212.
- N.M. Otway, C.J.A. Bradshaw and R.G. Harcourt [2004], *Estimating the Rate of Quasi-Extinction of the Australian Grey Nurse Shark (Carcharias taurus) Population Using Deterministic Age- and Stage-Classified Models*, Biol. Conserv. **119**, 341–350.
- R.H. Peters [1983], *The Ecological Implications of Body Size*, Cambridge Univ. Press, Cambridge, UK.
- S.L. Pimm, H.L. Jones and J. Diamond [1988], *On the Risk of Extinction*, Amer. Natur. **132**, 757–785.
- R.E. Rainbolt and B.E. Coblenz [1997], *A Different Perspective on Eradication of Vertebrate Pests*, Wildlife Soc. Bull. **25**, 189–191.
- D.J. Rapport [1998], *Ecosystem Health, Ecological Integrity, and Sustainable Development—Toward Consilience*, Ecosys. Health **4**, 145–146.
- D.H. Reed, J.J. O’Grady, J.D. Ballou and R. Frankham [2003], *The Frequency and Severity of Catastrophic Die-Offs in Vertebrates*, Animal Conserv. **6**, 109–114.
- M.G. Ridpath and J. Waithman [1988], *Controlling Feral Asian Water Buffalo in Australia*, Wildlife Soc. Bull. **16**, 385–390.

J.P. Rodriguez [2000], *Impact of the Venezuelan Economic Crisis on Wild Populations of Animals and Plants*, Biol. Conserv. **96**, 151–159.

A.A. Sharov and A.M. Liebhold [1998], *Bioeconomics of Managing the Spread of Exotic Pest Species with Barrier Zones*, Ecol. Appl. **8**, 833–845.

S.J. Song and R.M. M'Gonigle [2001], *Science, Power, and System Dynamics: The Political Economy of Conservation Biology*, Conserv. Biol. **15**, 980–989.

D. Spielman, B.W. Brook and R. Frankham [2004], *Most Species Are Not Driven to Extinction before Genetic Factors Impact*, Proc. Natl. Acad. Sci. **101**, 15261–15264.

D.W. Stephens, W.J. Sutherland and R.P. Freckleton [1999], *What is the Allee Effect?*, Oikos **87**, 185–190.

P.A. Stephens and W.J. Sutherland [1999], *Consequences of the Allee Effect for Behaviour, Ecology and Conservation*, Trends Ecol. Evol. **14**, 401–405.

J.A. Thomas, M.G. Telfer, D.B. Roy, C.D. Preston, J.J.D. Greenwood, J. Asher, R. Fox, R.T. Clarke and J.H. Lawton [2004], *Comparative Losses of British Butterflies, Birds, and Plants and the Global Extinction Crisis*, Science **303**, 1879–1881.

G.R. Tracy and P.F. Brussard [1996], *The Importance of Science in Conservation Biology*, Conserv. Biol. **10**, 918–919.

O. Ullsten and D.J. Rapport [2001], *On the Politics of the Environment: Ecosystem Health and the Political Process*, Ecosys. Health **7**, 2–6.

L. von Bertalanffy [1938], *A Quantitative Theory of Organic Growth*, Human Biol. **10**, 181–213.

D.S. Wilkie and J.F. Carpenter [1999], *The Potential Role of Safari Hunting as a Source of Revenue for Protected Areas in the Congo Basin*, Oryx **33**, 339–345.

E.A. Wilman [1996], *Pests—Sustained Harvest versus Eradication*, J. Environ. Manage. **46**, 139–147.

E.O. Wilson [1998], *Consilience: The Unity of Knowledge*, Alfred A. Knopf, New York.

T.P. Young [1994], *Natural Die-Offs of Large Mammals—Implications for Conservation*, Conserv. Biol. **8**, 410–418.