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Spatially explicit spreadsheet modelling for optimising the efficiency of reducing invasive animal density

Clive R. McMahon[1], **Barry W. Brook**[2], **Neil Collier**[1] **and Corey J. A. Bradshaw***[2,3]

[1]School for Environmental Research, Institute of Advanced Studies, Charles Darwin University, Darwin, NT 0909, Australia; [2]The Environmental Institute and School of Earth Environmental Sciences, University of Adelaide, Adelaide, SA 5005, Australia; and [3]South Australian Research and Development Institute, P.O. Box 120, Henley Beach, SA 5022, Australia

Summary

1. Invasive ungulates with eruptive population dynamics can degrade sensitive habitats, harbour disease-causing pathogens and facilitate the spread of weedy plants. Hence there is a need globally for cost-effective density reduction and damage mitigation strategies. User-friendly software tools that facilitate effective decision making by managers (who are not usually scientists) can help in understanding uncertainty and maximising benefits to native biodiversity within a constrained budget.

2. We designed an easy-to-use spreadsheet model – the Spatio-Temporal Animal Reduction (STAR) model – for strategic management of large feral ungulates (pigs, swamp buffalo and horses) within the World Heritage Kakadu National Park in Australia. The main goals of the model are to help park managers understand the landscape and population dynamics that influence the number and distribution of feral ungulates in time and space.

3. The model is a practical tool and methodological advance that provides a forecast of the effects and financial costs of proposed management plans. Feral animal management in the park is complex because populations cover an extensive area comprised of diverse and difficult-to-access habitats. There are also large reservoir populations in the regions surrounding the park, and these can provide immigrants even after within-park control operations. To provide the optimal outcomes for the reduction of feral animals, STAR is spatially explicit in relation to habitat, elevation and regions of culling, and applies density-feedback models in a lattice framework (multi-layer grid) to determine the optimal cost–benefit ratio of control choices. A series of spatial and nonspatial optimisation routines yielding the best cost–benefit approaches to culling are provided.

4. The spreadsheet module is flexible and adaptable to other regions and species, and is made available for testing and modifying. Users can operate STAR without having prior expert knowledge of animal management theory and application. The intuitive spreadsheet format could render it effective as a teaching or training tool for undergraduate students and landscape managers who might not have detailed ecological backgrounds.

Key-words: asian swamp buffalo, cost–benefit, culling, density dependence, dispersal, economic, functional response, horse, optimisation, pig

Introduction

Invasions of non-indigenous species into sensitive regions today represent major threats to biodiversity, ecosystem sustainability, agricultural efficiency and human health (Blackburn & Duncan 2001; Edwards *et al.* 2004; Hampton *et al.* 2004). Indeed, invasive vertebrate species are contributors to (i) the spread and maintenance of zoonotic, wildlife and agricultural disease (Barlow 1996; Caley & Hone 2004; Doran & Laffan 2005; Corner 2006); (ii) the physical destruction of rangelands (Bowman & McDonough 1991; Bowman & Panton 1991; Hone 1995; Corbett & Hertog 1996); (iii) the proliferation and spread of weedy plants

*Correspondence author. E-mail: corey.bradshaw@adelaide.edu.au
Correspondence site: http://www.respond2articles.com/MEE/

(Cowie & Werner 1993; Fensham & Cowie 1998; Buckley *et al.* 2004) and (iv) the direct predation or reduction of native species (Corbett & Hertog 1996; Courchamp & Sugihara 1999; Courchamp, Langlais, & Sugihara 2000). Each system within which invasive species have become established presents its own suite of complexities; however, one of the few generalizations is that non-native species elicit the greatest negative impacts when they perform an entirely novel function in the recipient biological community (Ruesink *et al.* 1995; Parker *et al.* 1999). However, attributes of the invader and the biological community it invades can regulate the severity and impacts of the invasion (Sakai *et al.* 2001); therefore, both the direct control of the invasive species and the manipulation of the community itself can contribute to a reduction in damage (Buckley *et al.* 2004).

Invasive species control generally attempts to decrease the numbers of the pest population(s) below some predefined critical 'damage threshold' (Shea *et al.* 1998). The challenge then is to predict not only the management strategies that will be effective in achieving the desired threshold density (Buckley *et al.* 2004), but the acceptable level of damage and its relationship to pest density (Hone 1995; Edwards *et al.* 2004). Additionally, the ability of the target population(s) to recover, and how the other components of the invaded ecosystem will respond, also need to be assessed (Buckley *et al.* 2004). Thus, an understanding of the spatial structure, dispersal capacity and population genetics of the pest species is usually required for effective control (Edwards *et al.* 2004; Hampton *et al.* 2004). However, density reduction or eradication of invasive species is complicated by various conflicting scientific and socioeconomic agendas (Myers *et al.* 2000; Brook *et al.* 2003; Bradshaw & Brook 2007; Albrecht *et al.* 2009).

In Australia, a variety of introduced plant and animal species pose serious threats to the long-term maintenance of rangeland biodiversity (Edwards *et al.* 2004). The challenge of controlling vertebrate invasive species is particularly high in the remote regions of Australia where large areas, harsh climates and cryptic animal behaviour inhibit control efforts. Scientifically backed management is especially important for maintaining environmental stability and biodiversity in sensitive areas of global biodiversity significance such as Kakadu National Park (Australian Greenhouse Office 2005). Kakadu National Park covers 19 804 km^2 and is situated in the monsoon tropics of the Northern Territory (Fig. 1). The diversity of different plants and animals within the park and the ways in which they are associated reflect the global importance of the geological and landscape diversity. Due to this variation in landscape, vegetation and animal species, Kakadu boasts some of the greatest natural and cultural diversity in Australia, hence its World Heritage status (Bradshaw *et al.* 2007).

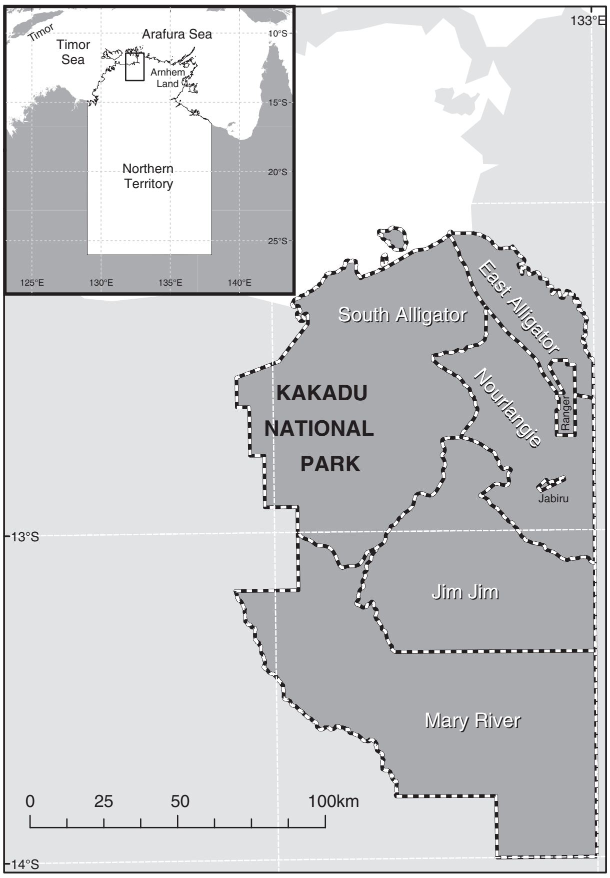

Fig. 1. The location of Kakadu National Park in the Northern Territory, Australia and its six management districts (South Alligator, East Alligator, Nourlangie, Ranger, Jabiru, Jim Jim and Mary River) that include the uranium mine site (Ranger) within the park. See also Google Maps link http://maps.google.com/maps?t = h&hl = en&ie = UTF8&ll = -12.993611,132.61846&spn = 4.71435,7.630005&z = 8.

Currently within Kakadu there are many invasive plant and animal species. Of these, the greatest threats to biodiversity are arguably some of the introduced weedy plants (e.g. *Mimosa pigra* Cowie & Werner 1993) and a variety of feral vertebrate herbivores (Bradshaw *et al.* 2007). Of the latter, Asian swamp buffalo (*Bubalus bubalis*), pigs (*Sus scrofa*) and horses (*Equus caballus*) represent perhaps some of the greatest challenges to protection of the landscape and biodiversity (Letts 1979; ANPWS 1991; Skeat, East, & Corbett 1996) through their role as introducers and spreaders of weed plants' seeds, over-grazers of native species, modifiers of vegetation communities and landscape transformers (Cook, Setterfield, & Maddison 1996; Bradshaw *et al.* 2007). However, controlling the densities of these animals is difficult given the size and range of habitats within the park and the consequent paucity of knowledge with respect to the distribution of the animals and the cross-cultural views reflected in its management (Bradshaw *et al.* 2007; Albrecht *et al.* 2009).

The suppression of feral animals in the Northern Territory has always been difficult for three main reasons: (i) the species considered most problematic have large populations within the region, necessitating substantial, broad-scale and highly coordinated approaches; (ii) the cost of control increases with decreasing animal densities (Bayliss & Yeomans 1989; Choquenot, Hone, & Saunders 1999) and (iii) the remoteness and rugged terrain makes access, logistics and practical approaches to culling challenging and expensive (Bradshaw *et al.* 2007). Past control has therefore been generally *ad hoc*, expensive and largely unsuccessful (Bayliss & Yeomans 1989; Choquenot

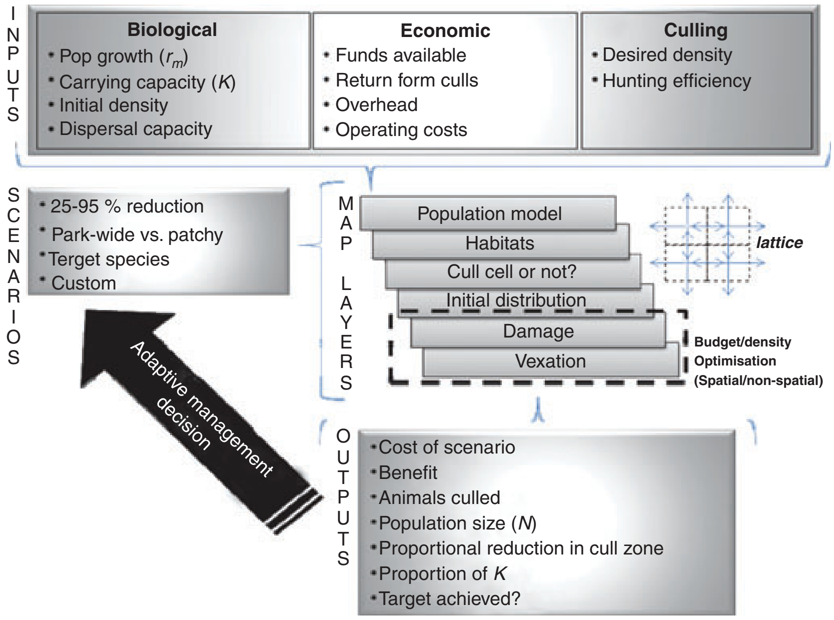

Fig. 2. The conceptual structure for the Microsoft Excel®, interactive spreadsheet-based feral animal management model.

et al. 1999). Further, there has been little follow-up monitoring.

Numerical models can facilitate efficient long-term control by combining information on population dynamics, economics and landscape configurations to identify effective removal strategies for optimal management planning (Sharov & Liebhold 1998; Rodriguez 2000; Haule, Johnsen, & Maganga 2002; Bradshaw & Brook 2007) and updating control strategies as new knowledge is obtained (ideally, via ongoing data analysis of the control effort). Spatial models also have the capacity to inform managers on the movement of immigrant individuals into control areas so that the appropriate culling regimes take immigration gains into account. Habitat-based models also give information about population densities relative to habitat type so that managers can target prescribed areas for the most efficient culling.

Within any strategic approach to pest management, there is a need to minimise the cost–benefit ratio of removal (i.e. a desired reduction in damage through the removal of individuals relative to the cost of removing them) and to minimise the damage to habitat within finite budgetary limits (Hone 1994). To enable an optimal approach within a decision-based management framework requires modelling the important ecological, damage limitation and economic factors to explore and provide a suite of optimal cost–benefit outcomes. In this paper we describe a user-friendly spreadsheet modelling tool called the 'Spatio-Temporal Animal Reduction' (STAR) model that we constructed specifically for Kakadu National Park for effective feral animal management planning. This tool provides a practical means of exploring the biological, logistical and financial consequences of alternative conservation management scenarios in a virtual landscape (Dunning *et al.* 1995; Macdonald & Rushton 2003), and could be readily modified to suit other regions and species.

The primary use of the STAR model is as a heuristic rather than predictive tool; it is not intended for projecting absolute costs and expected density reductions. Instead, it provides informed comparisons of different scenarios to (i) provide the minimum proportion of the population of feral animals needed to be culled for effective control; (ii) identify which habitats and in which configuration optimal culling regimes should be planned; (iii) provide relative information regarding the spatial and temporal cost of feral animal density reduction and (iv) provide a means of incorporating new data acquired from monitoring, experimental manipulation of densities, environmental damage assessment and changing socioeconomic conditions into a single framework for optimum landscape management.

Methods

TARGET SPECIES

The most conspicuous exotic animals in northern Australia derive from populations introduced in support of early European settlements, and in the subsequent development of agriculture there (Bradshaw *et al.* 2007). The first settlement at Fort Dundas on Melville Island (Tiwi Islands) had by 1826 a complement of stock including cattle (*Bos* spp). Asian water buffalo *Bubalus bubalis*, pigs *Sus scrofa*, goats *Capra hircus* and sheep *Ovis aries*. A year later buffalo, pigs, banteng *Bos javanicus* and horses *Equus caballus* were introduced to the mainland at Raffles Bay, Cobourg Peninsula and released when the settlement was abandoned 2 years later (Albrecht *et al.* 2009). Some of these species have proliferated in the Northern Territory, achieving densities higher than ever seen in their native habitats (Freeland 1990; Bradshaw *et al.* 2006).

Pigs

World-wide, but particularly in Australia, feral pigs *Sus scrofa* (Linnaeus 1758) threaten biodiversity, agriculture and public health (Bowman & Panton 1991; Machackova *et al.* 2003; Vernesi *et al.* 2003; Caley & Hone 2004; Hampton *et al.* 2004; Fordham, Georges, & Corey 2006). Feral pigs are now found across approximately 40%

of Australia because of natural expansion, intentional release and escapes or abandonment. In the 1990s, there were an estimated 13–23 million feral pigs in Australia (Hone 1990) but their range is still increasing in many regions (Cowled *et al.* 2009). Densities can range from 0·1 to >20 km^{-2} (Choquenot, McIlroy, & Korn 1996). Feral pigs are a major pest of agricultural crops in Australia (costing $>$ AU\$100 million annually) and carry a number of diseases and parasites of economic importance to livestock industries (Hampton *et al.* 2004; Corner 2006). The species also acts as a transmission vector for a number of endemic and exotic diseases capable of affecting livestock, wildlife and people, including leptospirosis and brucellosis, foot-and-mouth disease and Japanese encephalitis (Choquenot *et al.* 1996; Dexter 2003; Caley & Hone 2004).

Buffalo

After the collapse of the buffalo hide industry in the 1950s, an unrestricted population explosion caused severe damage to the lowland environment (Cowie & Werner 1993; Corbett & Hertog 1996; Skeat *et al.* 1996; Werner 2005; Liddle *et al.* 2006; Werner, Cowie, & Cusack 2006) which has only partially recovered in recent years. Between 1980 and 1989, approximately 80 000 buffalo were removed from Kakadu and surrounding regions as part of the Brucellosis and Tuberculosis Eradication Campaign (BTEC; Skeat 1990; Corbett & Hertog 1996; Skeat *et al.* 1996; Petty *et al.* 2007). Another 20 000 remained in the park and numbers were reduced to approximately 250 when the BTEC programs ended in 1996 (Skeat 1990; Corbett & Hertog 1996; Skeat *et al.* 1996; Petty *et al.* 2007). Being large, heavy animals (up to 800 kg for females and 1200 kg for males; Moran 1992) that consume up to 30 kg of food day^{-1}, and with a tendency to have restricted movements (Tulloch 1969; Ford 1978), damages to vegetation, water courses and soils are high (Cowie & Werner 1993; Corbett & Hertog 1996; Skeat *et al.* 1996; Werner 2005; Liddle *et al.* 2006; Werner *et al.* 2006). Although densities were estimated to be $<$ 0·1 km^{-2} in the early 1990s (Skeat 1990), the Kakadu landscape has been able to support densities up to 34 km^{-2} (Ridpath *et al.* 1983).

Horses

Feral horses are relatively common in the Northern Territory, but are less abundant than buffalo in Kakadu or donkeys in the subhumid tropics (Graham *et al.* 1982; Graham, Johnson, & Graham 1986; Bayliss & Yeomans 1989). Horse populations can increase by 20% year^{-1} under favourable conditions and mortality is mainly due to drought and human control (Dobbie, Berman, & Braysher 1993). In Kakadu, sites with unusually high densities of horses are often associated with places where they were used in large numbers to support the pastoral industry or buffalo hunting, or were sometimes raised for sale (McLaren & Cooper 2001). Although damage caused by feral horses has never been studied directly in northern Australia, they are known to contribute to erosion, damage vegetation and disperse weeds (Letts 1979; Dobbie *et al.* 1993). Horses are also potential reservoirs for human and animal disease, including melioidosis (Cheng & Currie 2005), Kunjin virus (Mackenzie, Smith, & Hall 2003) and Bunya virus (Weir 2002).

MODEL STRUCTURE

The STAR model was designed as a user-friendly, yet ecologically realistic tool for the management of feral animal populations in Kakadu National Park. The model was written as an interactive Microsoft Excel® (www.microsoft.com) spreadsheet model using Visual Basic for Applications (VBA) language (see Appendix S1 for a detailed User Manual and Appendix S2 for the VBA code). We specifically chose to use VBA because the programming language is relatively simple and native to Excel, it provides an ideal vehicle for developing windows-based applications such as our interactive spreadsheets and it can provide a graphical user interfaces within Excel that makes it easy to connect to functions provided by the application. We also specifically chose the spreadsheet format because of its familiarity to nonmathematical personnel, ubiquity and visual appeal. These criteria are especially important when providing a tool for general use by non-experts such those involved with on-ground wildlife management. The model is based on the landscape configuration of the park and is thus spatially explicit with respect to habitat type, elevation and districts (Fig. 1 & 2). The model structure uses density-feedback and economic cost functions (see Cell Mechanics & Control Layers sections below) to determine the cost–benefit ratio of proposed control scenarios.

The spatial and temporal variation in suitable habitat over entire landscapes also influences distribution and abundance. Feral animal density is represented as a numerical response of the interactions between the: (i) specific habitat's carrying capacity; (ii) rate of recruitment (fertility and survival to breeding age); (iii) rate of immigration and emigration (dispersal); (iv) culling rate (human-induced mortality) and (v) spatial and temporal variation in the landscape (habitat availability, configuration and change). These parameters are the basis for any spatially explicit population reduction model; however, for it to be useful for management, the following socioeconomic factors also need consideration: (i) the time-frame for population reduction (e.g. whether the exercise is a single treatment, to be sustained or a sporadic exercise); (ii) the regions targeted for control (i.e. control over an entire landscape or specific target areas); (iii) whether commercial benefits can be derived from the harvested animals (e.g. meat production, safari income; Bradshaw & Brook 2007) and (iv) the cost of culling itself (e.g. helicopter time, salaries, consumables).

The following sections outline some of the more important mechanics of the STAR model, with particular emphasis placed on how it can be manipulated by the user (see also Appendix S1 – User Manual). In particular, the types of culling scenarios that can be implemented are discussed with respect to their relative effectiveness at achieving target densities and budgets. Following these comparisons, a more detailed explanation of various optimisation subroutines are provided (see below) to demonstrate how complex spatial and temporal decision making can be enhanced by informed use of the STAR model.

Cell mechanics

Many forms of discrete-time, density-feedback population models that synthesise demographic information (Brook *et al.* 2003) have been developed to prescribe the most effective management options for density reduction and eradication in particular areas (e.g. Buckley *et al.* 2004), with many focusing on the optimal control programs for disease management (Saunders & Bryant 1987; Pech & McIlroy 1990; Dexter 2003; Doran & Laffan 2005). Many such models divide the target area into discrete units so that each becomes a separate time-series projection in its own right (Akçakaya & Brook 2008; Highfield *et al.* 2009; Ward, Laffan, & Highfield 2009). These units (or cells) do not usually act independently; if individuals are allowed to move into adjacent cells, then the dynamics within that cell will differ quantitatively from a cell that has no input from or output to adjacent cells.

We modelled the spatial structure of STAR on a 10 × 10 km cell grid of the entire park (cellular lattice framework; Fig. 2). Thus, park, district and habitat boundaries are approximations of their real-world coordinates and some spatial resolution is lost. This reduction in spatial grain was necessary because finer-scale outputs are limited by data availability (but the grain could be made finer with the collection of finer-resolution data or application of the model to different areas with analogous problem species). Each cell within the grid thus acts as a particular unit within the overall dynamics of the park, and the summary information provided at the end of a simulation is an overall expression of all cells.

The change in animal numbers within each cell is governed by the following expression:

$$N_{i,j,t+1} = N_{i,j,t} e^{r_m\left[1-\left(\frac{N_{i,j,t}}{K_{i,j}}\right)^{\theta}\right]} - C_{i,j} - (E_{i,j} - I_{i,j}), \qquad \text{eqn 1}$$

where i is the cell row number in the 10 × 10 km grid, j is the cell column number, t is the time interval (consecutive wet–dry season), $N_{i,j,t+1}$ is the number of animals in cell i,j at the next time interval ($t + 1$), $N_{i,j,t}$ is the number of animals in cell i,j at time interval t and r_m is the maximum rate of population increase when resources are not limiting: this value differs among species and is a function of survival probability and fecundity (Appendix S1). For example, pigs have a high r_m given their ability to produce multiple large litters annually (estimated using allometric predictions; Bayliss & Yeomans 1989), $K_{i,j}$ is the habitat-specific maximum carrying capacity; we set K to the maximum values observed for the species examined from various areas throughout northern Australia (Graham *et al.* 1982; Bayliss & Yeomans 1989; Freeland 1990), θ is a shape parameter that modifies the relationship between r and population size (N). Although estimating θ using only time series of abundance is problematic (Polansky *et al.* 2009), applying this parameter in the above expression controls the population's rate of response to K; a θ value >1 implies that density feedback operates most strongly close to carrying capacity, whilst $\theta < 1$ indicates a stronger effect of density at low numbers and has strong ecological-demographic foundation (Owen-Smith & Mills 2006), $C_{i,j}$ is the total number of animals culled in cell i,j (depends on the culling rate set by the user and represents the total number of animals killed at each time step), $E_{i,j}$ is the total number of animals emigrating from cell i,j (depends on the movement probability set by the user; it represents the total number of animals moving out of cell i,j at each time step) and $I_{i,j}$ is the total number of animals immigrating into cell i,j (depends on the movement probability set by the user; it represents the total number of animals moving into cell i,j from its surrounding cells at each time step).

The expression predicts a new population size as a function of its intrinsic capacity to grow, the number of individuals killed during a particular time interval and the number of animals moving in and out of the cell of interest. Taking summaries of each main element provides the total number of animals present at the beginning of a culling regime, the total remaining after the control has occurred, the number of animals harvested and the final spatial configuration of the remaining population within the park. Initial densities can be adjusted via the 'initial fraction of K' modifier which sets start densities as a proportion of carrying capacity, by limiting initial distribution in the 'Distribution' layer, and by changing the suitability of each habitat type's K itself (see Appendix S1).

We also included the capacity to test the sensitivity of model projections to variation in certain parameter values. The user can set a desired uncertainty as a percentage of the mean (inputted value; limited to 1–50%) in the maximum growth rate (r_m), carrying capacity (K), theta parameter in the θ-logistic model (θ), the escarpment K modifier and the escarpment dispersal modifier (see User Manual and below for more details). The user can then choose whether a particular parameter from the list above is taken from the lower, mean or upper end of this set uncertainty range (via a drop-down menu). Sensitivity of model projections to other parameters with currently more uncertainty (e.g. relative habitat suitability, dispersal probability and functional response) could be assessed manually by modifying parameters based on a range of plausible values entered manually by the user.

Control layers

The STAR model includes a map layer where the user can prioritise whether or not a cell should be culled based on a combination of known or suspected damage caused by feral animals and the user's understanding of the sociopolitical sensitivities in each area of the park (Fig. 2).

Damage. We calculated an index of landscape-scale damage caused by feral animal populations within Kakadu (e.g. spread of weeds, over-grazing, soil compaction, topsoil disturbance, etc.) compiled from various consultations with Kakadu rangers, administrators, Aboriginal traditional owners and others familiar with the park (Field, Bradshaw, & Haynes 2006). Although we have provided a preliminary summary of this attribute, damage is a highly dynamic property of the landscape and can be modified by the user accordingly. With more information (e.g. from aerial surveys, on-site inspections, etc), the map can be adjusted.

Vexation. We included a user-defined spatial layer that can incorporate a relative scale of 'management vexation' for each cell in Kakadu. In essence, the greater the vexation value of a cell, the more difficult it is to implement a culling regime due to various stakeholder concerns. This layer is provided initially with absolutely no assumption about the level of vexation. The user can modify these cells according to his or her perceptions or measured values of vexation in the park, especially after local management interventions that might elicit particularly strong supportive or negative responses from stakeholders. Each cell can receive one of three qualitative values: 0 = no vexation, 1 = moderate vexation and 2 = high vexation. For example, the cells incorporating the Jabiru township (Fig. 1) or a sacred Aboriginal site might receive a '2' for an aerial buffalo shoot given the potential danger to people on the ground or to the possibility of damaging sacred landscape features. The combination of damage and vexation layers is contingent on the application of a priority matrix that indicates combinations of damage and level of vexation that lead to a hierarchical listing of priority (Table 1). For instance, if the management vexation of a cell is low (e.g. 0) and the damage from feral animals is high (e.g. 2), then that cell receives a high-priority rating (e.g. 5). This priority layer then modifies the cost–benefit scores on which the entire optimisation routines are based (see Optimisation section).

Table 1. The hierarchical listing that combines the damage and vexation layers determined from a priority matrix

	Vexation		
Damage	**0**	**1**	**2**
0	1·0	1·0	1·0
1	4·0	3·0	2·0
2	5·0	4·0	3·0

Bioeconomics. The STAR model incorporates various economic components, but it is not a formal economic analysis. However, the model provides a useful relative index of the magnitude of change in budgets required for particular culling scenarios. Implicit in this idea of a cost-per-unit-time approach is the functional response (culling efficiency); search time increases as populations become smaller (Bayliss & Yeomans 1989; Cowled *et al.* 2006). Another consideration is the potential to recoup revenue derived from selling either the products derived from the culls (e.g. meat) or the privilege of being involved in the culling process (e.g. safaris). The model allows the user to specify a particular per-culled-individual revenue stream that can offset the total costs required for a particular control program.

The STAR model combines these cost and revenue layers into a spatially explicit cost–benefit score upon which the various optimisation routines are based (see Optimisation section). The first component of this is the cell-based cost function which estimates the total cost (C) per cell as:

$$C = H \times V \times a\left(\frac{N}{A}\right)^{b}, \qquad \text{eqn 2}$$

where H is the hourly cost of helicopter (or ground-based) hire, V is the overhead cost of implementing culling, a is the hunting efficiency intercept taken from the relationship between hunting time and animal density (Bayliss & Yeomans 1989; Freeland & Choquenot 1990; Boulton & Freeland 1991), N is the number of animals cell^{-1} in a particular season, A is the area of cell (i.e. 10×10 km = 100 km^2) and b is the hunting efficiency slope (Bayliss & Yeomans 1989).

The optimisation routines are in part modified by the final expression of cost relative to the benefit derived from the culling regime. In this case, the benefit is defined as the relative reduction of feral animals within a grid cell, weighting more positively for cells with high initial densities prior to culling. Thus, benefit is maximised due to relative changes in density (e.g. if a particular cell with a high density of animals was reduced to low numbers, rather than a cell where densities were naturally low). Costs and benefits are then compiled into a single parameter defined here as the cost–benefit (γ) score:

$$\gamma = \frac{C \times T \times n_c}{B \times P}, \qquad \text{eqn 3}$$

where C is the total cost of culling cell^{-1} year^{-1}, T is the duration of the model run in years, n_c is the total number of cells being culled in the control area, B is the total budget available for the cull and P is the priority composite score derived from the damage and vexation maps measured across the entire target control region.

Optimisation

The three optimisation routines in STAR are among the most powerful and potentially useful features of the application because they allow a financially and logistically constrained decision maker to determine an 'optimal' management approach. In other words, the optimisation routines allow managers to achieve the greatest density reductions for a given budget, they indicate the magnitude of budget required for a given density reduction target, or they indicate which areas are the most efficient to cull. Optimisation therefore includes explicit consideration of the following trade-offs: (i) a finite budget; (ii) a density goal and (iii) a spatial goal (i.e. an area from which animals are identified *a priori* for removal). These optimisation routines are triggered via buttons on the *inputs* worksheet. However, the optimisation routines are reliant on what the user sets in the *vexation* and the *damage* layers (Appendix S1). These are combined in a priority matrix (Table 1) which then modifies the cost–benefit scores in the *bioeconomics* layer (Appendix S1). Thus, the optimal budgetary, density and spatial configurations are sensitive to the damage and vexation inputs that are originally defined. Two of the three optimisation routines are nonspatial, and for simplicity in all three routines, the proportional initial cull (first year) is set to be the same as the maintenance cull (subsequent years).

For the two nonspatial routines, the user can choose either to find (i) the maximum proportional cull rate that can be achieved for a set of target landscape cells (designated in the *culling* worksheet) given a specified total budget or (ii) if a control area target density is specified, if the culling rate and budget required to achieve this target. In budget optimisation, the application iterates repeatedly, each time reducing the maximum and minimum cull rate search bounds, in systematically smaller increments until a value (set to the nearest percent, e.g. 60% or 61% are possible outcomes, whereas 60·2% is not) is found which matches the target budget. In general the routine requires far fewer than 98 trials to reach a solution (the theoretical maximum if all culling rates between 1% and 99% were trialled). The routine will also warn the user if either the specified budget is insufficient to cover the specified culling area at even marginal control rates (of 1%), or if maximum culling (of 99%) can be achieved for less than the specified budget (asking the user to expand the culling area or reduce the budget). The control area target density routine is similar, except that instead of the optimisation target being a fixed budget, the target is a density of animals per control cell. This routine will always produce a solution (at a cost – potentially a high cost at low target densities) unless the specified target density is higher than the carrying capacity or lower than that achievable with a 99% culling rate.

The spatial routine provides a partial optimisation based on minimising cost–benefit across a landscape within a budget. First, a target budget and set of target cells is specified by the user. Optimisation is then achieved by: (i) running a control scenario with culling rate set at 50% to populate the cumulative cost–benefit map and (ii) iterating through six percentiles (100%, 75%, 50%, 25%, 10% and 1%) of that map, and calling the nonspatial budget optimisation routine in each iteration. For instance, the 25th percentile would create a map of the cells that reflected the highest 25% of cumulative cost–benefit values for those cells that had been targeted for control (in the *culling* worksheet). After iteration, the scenario yielding the best density reduction in the control area, whilst staying within budget, is then output as an optimal cull rate and the final culling map; this scenario is then rerun. All optimisation VBA code is presented in Appendix S2.

Management scenarios

The STAR model has a suite of prespecified management scenarios that simulate plausible options for feral animal management. In general the scenarios we have designed fall into three main categories: (i) density targets that aim to reduce densities to specified targets over large areas; (ii) damage mitigation that aims to reduce damage in highly damaged and non-vexatious environments and (iii) optimised management that maximises profit from feral animal control while achieving reduction goals.

The STAR model provides 32 predefined scenarios that are subdivided by species (n = 14, 9 and 9 scenarios for pigs, buffalo and horses respectively). Within each of these major species categories, there are several different goals that each scenario attempts to achieve. These range from a zero culling rate to examine how populations will change over time with no management intervention, to those that cull a large proportion of the animals from the park and adjacent areas. Between these extremes are several example scenarios that have particular final target densities or those that focus on only certain districts within the park. The purpose of supplying informed, predefined scenarios is to provide managers with a flexible tool that accommodates a range of management options which are realistic in terms of the resources available.

Users can also provide their own customised management scenarios by adding details in the 'Prespecified management scenarios' list on the *inputs* worksheet. In the first customisable scenario row (Scenario 33), the user can add the target species, description of the scenario, initial cull rate, maintenance cull rate, control target density, initial density relative to K, years to run and culling map to use. For the latter, the user can specify an existing map from the *culling scenario maps* worksheet, or define a new one (we have provided two map templates – Maps 15 and 16 – scrolling to the far right of the *culling scenario maps* worksheet reveals these). If a customised map is required, the user places a '1' or a '0' in the appropriate cells in the customised map and specifies this in the scenario description on the *inputs* worksheet. Once the new scenario is loaded, these base parameters are used in the subsequent model run (see also Appendix S1).

We present the results arising from the implementation of a subset of these predefined scenarios to demonstrate the utility of the model's features for management decision making. For example, we address questions such as 'What are the costs associated with particular levels of culling?', 'What are the consequences of failing to cull outside the boundaries of a particular district destined for a culling program?', and 'Do district-limited culls achieve effective control, or are more density-targeted, park-wide culling programs necessary to achieve some longer-term reductions of density?'.

Specifically, we examined the following generalised scenarios: (i) large (75%) vs. small (25%) proportional culls of pigs; (ii) no-cull compared to a park-wide cull for buffalo; (iii) 75% reduction in pig density using spatially targeted (in areas of medium to high damage) and random (*ad hoc*) culls; (iv) targeted vs. district-limited culls of horses; (v) nonspatial vs. spatial optimisation for a single district cull of pigs with a constrained budget and (vi) nonspatial vs. spatial optimisation for a park-wide cull of pigs with a constrained budget.

Results

DENSITY TARGET SCENARIOS

Large vs. small proportional reductions

The first comparison explores how varying cull rates affect the total number of pigs within the park. We aimed to determine the culling strategy (cull rate year^{-1}) and associated costs required to achieve a 25% or 75% reduction in pig densities across the entire park over 10 years. In both scenarios, a 10-km buffer zone around the park was also included. For a 25% reduction, the desired target was achieved approximately 5 years into the program when culling in the first year was 17% and 9% thereafter (Fig. 3a). The total cost assuming helicopter fees of AU$1000 hour^{-1} and overheads of 18%, was just over AU$2·2 million (averaging AU$220 000 year^{-1}) to cull just over 90 000 pigs (AU$24 pig^{-1} on average). The maximum percentage reduction achieved was ~ 27%. However, a 25% reduction failed to reduce feral pig density substantially (Fig. 3b and c). Applying a 50% cull in the first year, followed by a 31% maintenance cull thereafter, reduced densities by the desired 75% target by year 10 (Fig. 3d), producing a noticeable park-wide reduction in densities (Fig. 3b and e). However, the associated costs were nearly five times greater (an additional AU$1·0 million year^{-1}), even though the total number of animals culled was only twice that from the 25% reduction given the constraints imposed by the reduced culling efficiency algorithm.

A simple example of estimating model output sensitivity to variation in parameter inputs is demonstrated using the 75% reduction model for pigs described above in this section. Using a 10% change in mean input parameter values, variation in r_m had the greatest effect on control area densities (1686–2632), followed by variation in habitat-specific K (1885–2181 remaining individuals), θ (1904–2114), escarpment K modifier (1957–2097) and finally, escarpment dispersal modifier (2018–2026). The low sensitivity of the final density to variation in the latter parameter is mainly due to relatively lower pig densities in the escarpment region. Of course, sensitivities will vary by species and control design/area chosen.

Zero vs. park-wide culls for buffalo

We compared not controlling buffalo with scenarios that had low and moderate cull rates over 10 years. We also restricted the initial distribution of buffalo based on recent estimates. STAR includes a distribution-restriction layer to indicate where the target species (i.e., buffalo, in this scenario) are currently thought to occur (Appendix S1). Here we assumed that all areas bordering the Park have buffalo present. We also set the initial proportion of $K = 0·5$; this sets the habitat-specific carrying capacities in the cells initially occupied by buffalo to 50% of maximum. The culling map used was 'No cull' to indicate a zero culling rate, and all other dispersal modifiers set for buffalo were used.

Not controlling buffalo numbers result in an increasing population over the next decade (Fig. 4a). With the initial parameters specified the buffalo population within the park more than doubles over the next 10 years (Fig. 4a). When compared to a moderate (20% initial cull followed by a 17% cull thereafter) park-wide (including the 10 km buffer outside the park) cull, the buffalo population size remains relatively constant (Fig. 4b) and costs approximately AU$5·0 million. Choosing not to cull outside park boundaries results in a slight increase in the population but costs less (AU$4·1 million; Fig. 4c). Increasing the budget by ~ 25% (AU$1·3 million) would allow for annual cull rates to be increased (e.g. 40% initially and 25% thereafter), resulting in a greater reduction in the population (Fig. 4d). This not only curtails population expansion it also results in a substantial reduction in overall park densities.

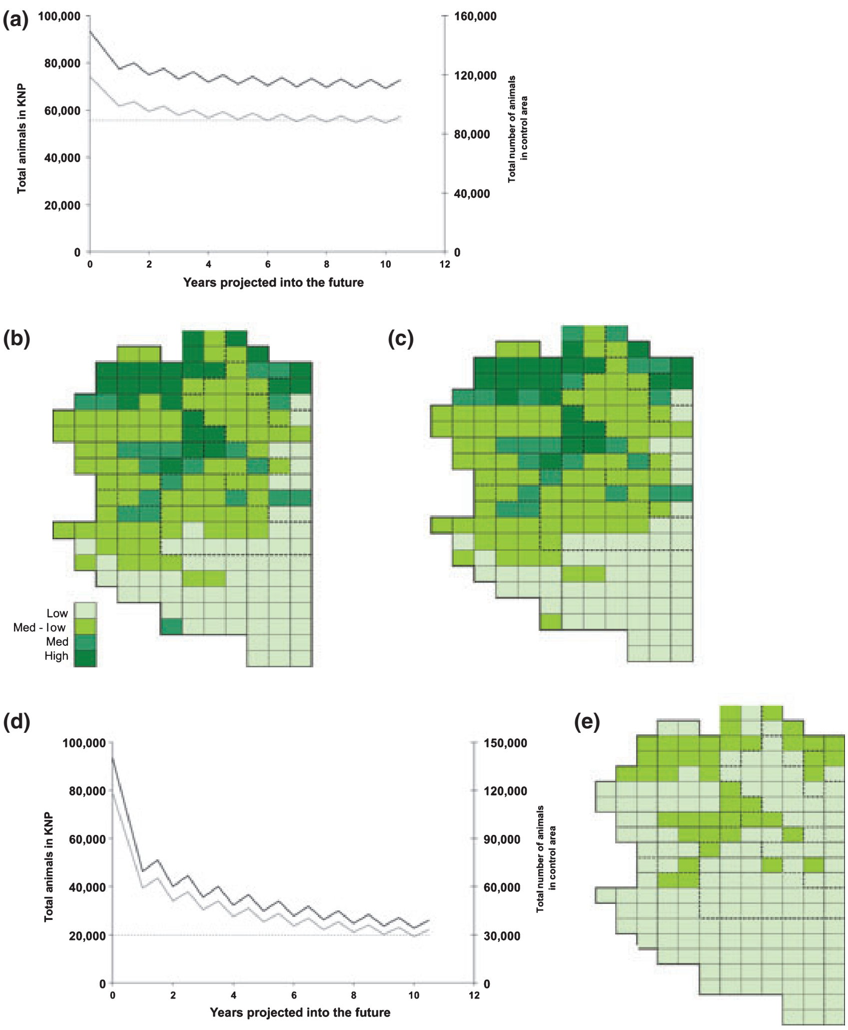

Fig. 3. Large vs. small population reduction strategies for feral pigs: (a) a 25% reduction in feral pig numbers (grey line: within the control area; black line: park-wide) was achieved using an initial cull (first year) of 17% of the total estimated population, with a maintenance cull of 9% thereafter, (b) a 75% reduction in feral pig numbers was achieved using an initial cull (first year) of 50% of the total estimated population, with a maintenance cull of 17% thereafter, (c) initial cell densities of feral pigs in the park before culling (d) final densities after a 25% reduction target is achieved and (e) final densities after a 75% reduction target is achieved.

DAMAGE MITIGATION STRATEGIES

Priority area vs. ad hoc *reductions*

We compared the effects of designating priority cull areas with random (*ad hoc*) spatial culls within the park to achieve a pig density reduction target of 75% over 10 years. The priority cull scenario designates areas as medium- and high-priority cells that are a function of the areas of vexation and damage layers (see Methods). For this example, we assumed that there are no particular areas of high or low vexation (i.e. all cell values in the vexation layer are set to 1); rather, cell priority is derived entirely from the damage layer (Fig. 5a).

Using this as the base cull layer, the initial culling rate is set at 50% of the total population in the first year, and 42% thereafter for the duration of the 10-year program. These culling rates and spatial configuration achieve the target 75% reduction in the control area and a total park-wide reduction of nearly 50% (Fig. 5b). The total cost of this scenario is just over AU$4·3 million with nearly 96 000 culled (i.e., AU$45 pig^{-1} on average). In comparison, the *ad hoc* (i.e. random, nonprioritised) culling strategy with similar culling rates (50% and 41% initial and maintenance cull rates, respectively) ends up costing slightly more (AU$5·0 million) than the prioritised cull strategy, but only 76 000 animals are culled in the *ad hoc* spatial configuration (Fig 5c). However, park-wide reduction is only 32% in total (compared to the 42% reduction using the prioritised strategy), and cost–benefit was much lower in the latter (0·05–0·06) than former (0·012–0·14) strategies (Fig. 5d and e), demonstrating the importance of choosing an appropriate spatial configuration for culling.

Effects of immigration and refugia

A more direct example of the implications of immigration into culled cells is shown by a comparison of a single-district management plan where the surroundings are included or excluded, or whether certain cells are left unmanaged (thereby acting as refugia; Fig. 6a and b). For this case study, we use pigs in the South Alligator district alone (Fig. 1). With an initial cull rate of 50% followed by 35% thereafter, we achieve a 75% reduction in this district after 10 years (total cost AU$2·1 million; AU$31 average cost individual^{-1}). Comparing this to a scenario where a 10 km buffer is also culled around the district reduces the necessary maintenance cull to 33% to achieve the same

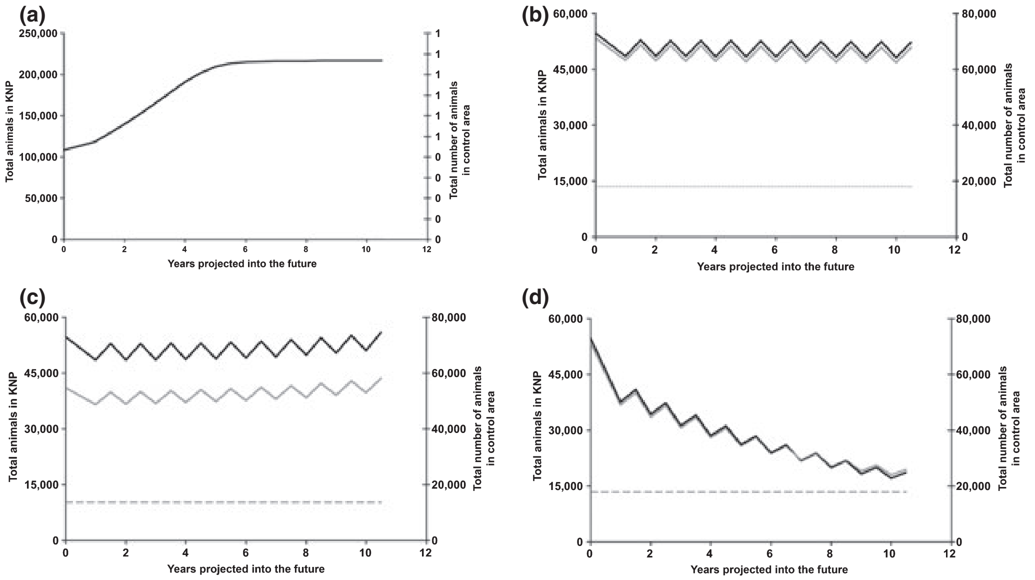

Fig. 4. Projections of the number of feral swamp buffalo resulting from (a) no culling, (b) a low culling program using a an initial cull of 20% followed by a maintenance cull rate of 17% year^{-1} and (c) a moderate culling program using an initial cull of 40% followed by a maintenance cull rate of 25% year^{-1}.

reduction target. However, this raises costs to AU$3·3 million (AU$34 individual^{-1} on average). Even though increasing the number of cells to be culled raises costs, this increase can be offset if the immigration rate from adjacent, non-culled cells is sufficiently high. The highest pig densities in the park are found initially in the South Alligator district (Fig. 1); therefore, the inclusion of a surrounding buffer (Fig. 6b) was not necessary because most of the effectiveness of the cull was already in place by including only those cells within the district.

The next example considers the effects of refugia within culling areas (Fig. 6c). This situation could arise if particular cells are considered too vexatious for control operations (e.g. sacred sites, areas of contestation, high-use tourist areas, etc.). Using the South Alligator district again, and based on a 50% initial culling rate and 35% maintenance cull, achieves a 75% reduction after 10 years (total cost AU$2·1 million). Removing six cells (refugia) from culling within this region requires increasing the maintenance cull to 40% to achieve the same 75% reduction, but total costs remain unchanged. Thus, the focal cells designated for culling require a higher annual rate of culling (40% vs. 35%) and the overall park-wide reduction of pigs is lower (69 000 vs. 66 000 remaining). This does not suggest that leaving refugia is always an inappropriate management strategy because (i) certain cells may be beyond negotiation when it comes to their level of vexation; (ii) not all refugia have high animal densities and (iii) small increases in annual culling effort might be achievable provided the total cost is not inflated unnecessarily due to animals emigrating from refugia to previously culled areas.

Finally, we considered a smaller district (Nourlangie, Fig. 1) with a lower initial pig population (Fig. 7a). Using 50% initial and 50% maintenance cull rates, we achieve a 75% reduction after 10 years for AU$2·2 million (Fig. 7b–d). However, the areas surrounding the Nourlangie district have high pig population densities that are likely to spill into Nourlangie at the cessation of culling (Fig. 7a). Expanding the culling area to include a few more cells outside of the target district where pig densities are high (additional 15 cells, or 150 km^2) reduces the minimum maintenance cull rate to 40% to achieve the same 75% control area target for a small increase in budget (AU$2·3 million). Not only has overall pig density been reduced, the entire district is now comprised of low-density cells (Fig. 7e).

Targeted vs. district-limited culls

In this scenario, we reduced the horse population within the Mary River district (Fig. 1), and then compared this strategy to one of identical effort that focuses culling in areas where horses are known to occur in the southern region of the park (Fig. 1) at an initial culling rate of 50% followed by 23% thereafter for 10 years. At this rate, we achieve a 75% reduction in the targeted district for AU$2·2 million (Fig. 8). We assumed a starting proportion of carrying capacity = 75%, so the total number of horses in the park increases slightly over the course of the culling program. Taking the same number of culling cells and shifting them into the areas known to have high densities of horses in the eastern and south-eastern section of the park (Fig. 1), and using the same initial (50%) and maintenance (23%) culling rates and starting initial proportion of carrying capacity (75%), 75% reduction is achieved. However, this results in a more effective reduction throughout the park (15%) for a marginal increase in budget (+AU$300 000).

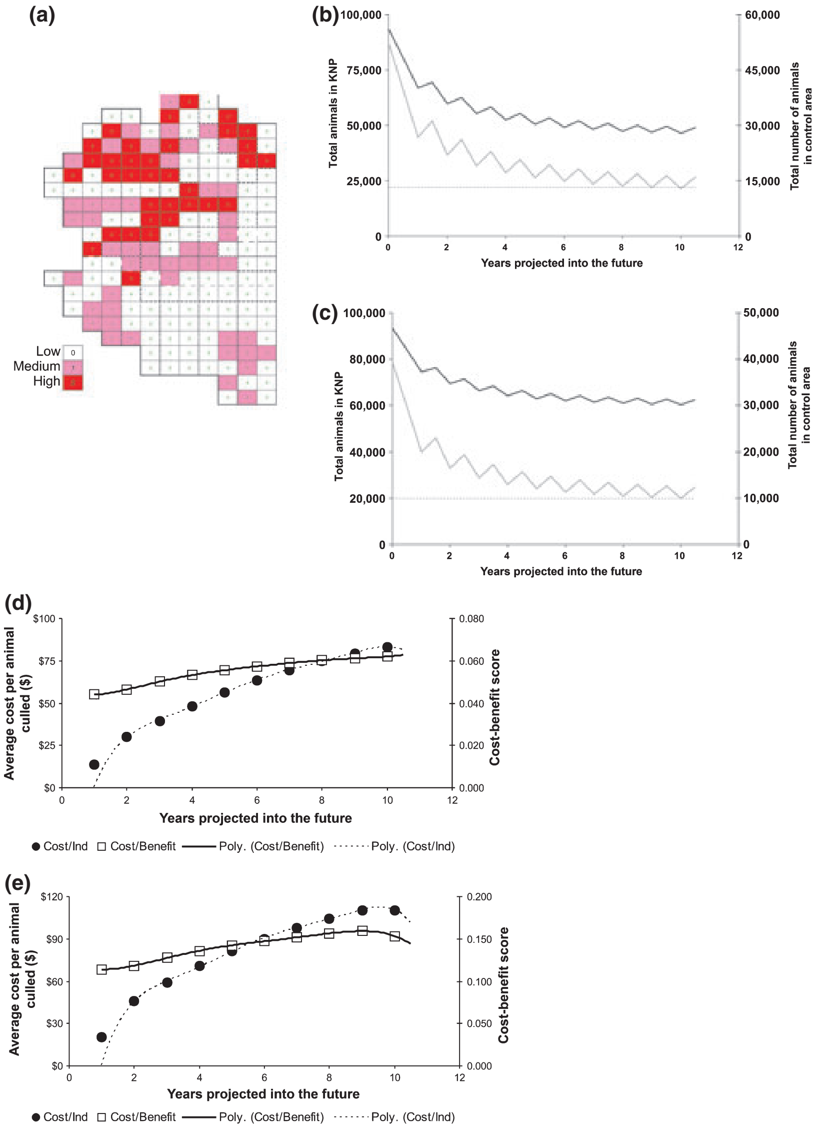

Fig. 5. The effects of priority area reductions compared with *ad hoc* reductions of feral pigs: (a) the culling priority areas based on levels of damage caused by feral vertebrates (low damage/priority = white cell squares; medium damage/priority = pink cell squares; high damage/priority = red cell squares), (b) projection of the number of pigs in the control area (grey line) and in the park (black line) using a priority cull strategy compared to (c) an *ad hoc* culling strategy, (d) the average cost of culling animals (AU$ individual culled^{-1}) and the cost–benefit score for the priority area culling strategy and (e) the *ad hoc* cull strategy.

OPTIMISED MANAGEMENT STRATEGIES

One of the most important components of any broad-scale feral animal reduction campaign is the normally prohibitive costs associated with culling. We therefore seek to minimise the cost–benefit score. Of course, reducing cost–benefit to zero implies no culling whatsoever, so a trade-off between cost and the number of animals culled is the parameter optimised. The benefit score against which cost is compared is the relative effectiveness of the cull measured as the proportional reduction of density cell^{-1}. This is further complicated by the fact that large reductions in cells originally containing high animal densities are more efficient than reductions in cells originally containing few individuals. Finally, the cost–benefit analysis only really pertains to the spatial optimisation routines because these allocate culling effort among cells of different starting densities. For the nonspatial optimisation, the most efficient culling attempts to maximise the total cull for the budget allocated, or find the most efficient cull rates over the set interval required to achieve a target density.

We present three types of optimisation: (i) finding the best culling strategies to attain a particular density (e.g. reducing pigs by 95%); (ii) finding the most efficient culling strategy within a predefined area for a particular budget and (iii) for a given budgetary goal, finding the optimal spatial arrangement of target cells to cull in the target area.

Optimising culling rates for a density goal

Although budget is essentially ignored in this case, certain optimal culling regimes targeting density goals in the most efficient manner often result in lower costs. The first example targets a

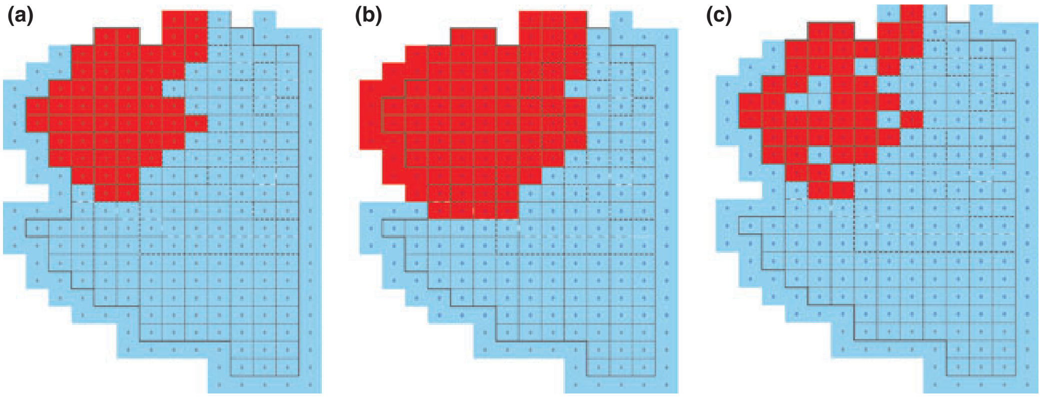

Fig. 6. Culling distribution maps for controlling feral pigs using (a) district targeted culls, (b) district targeted culls accounting for immigration of pigs from cells immediately surrounding the target district and (c) leaving some cells unmanaged.

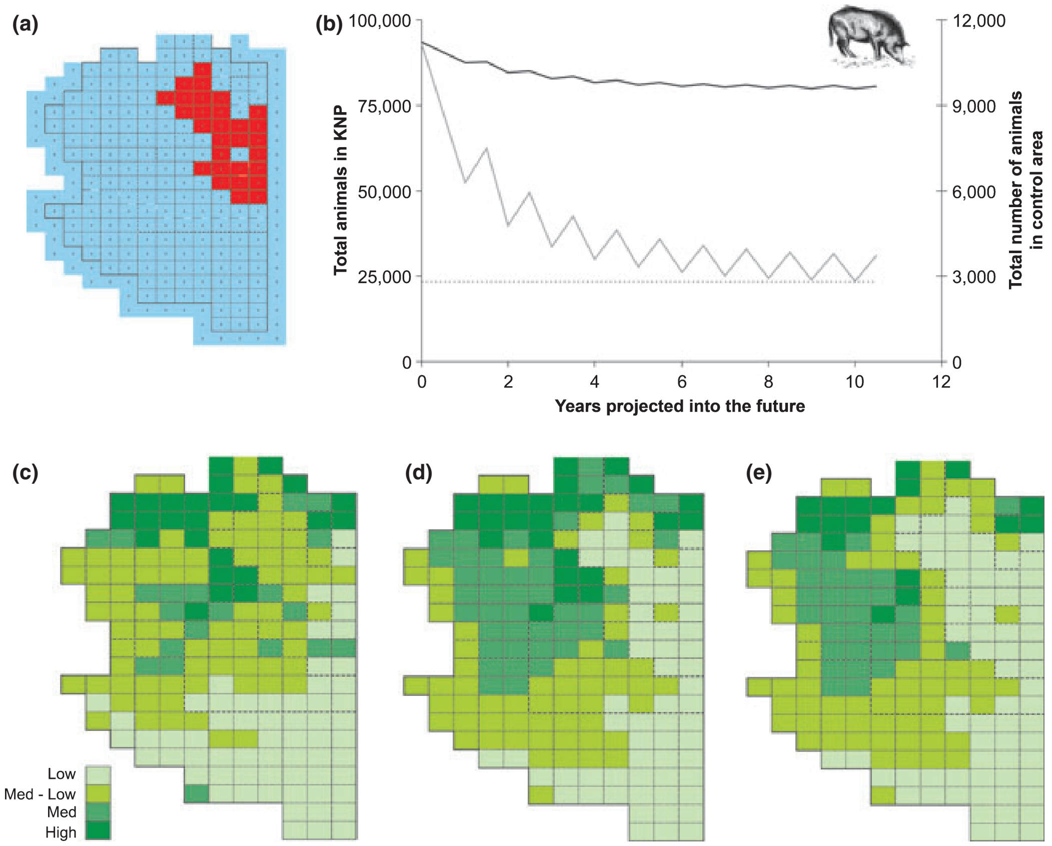

Fig. 7. Effectiveness of small district culling strategy on feral pigs: (a) The Nourlangie district control area (red squares) within the park, (b) a projection of pig population size in the control area (grey line) and in the entire park (black line), (c) pig densities across the park and the control area before culling, (d) pig densities across the park and the control area after district limited culling, and (e) pig densities across the park and the control area after culling in the district and the cells immediately surrounding the district.

75% reduction of horses within the Jim Jim district (Fig. 1) using an initial culling rate of 50% ($\sim$ 16 000 horses culled) and 26% thereafter ($K_1 = 0{\cdot}75K$). Total cost is AU\$1·23 million to cull 16 200 individuals (AU\$76 horse^{-1}; Fig. 9a). Keeping all other parameters in the latter scenario the same and invoking the nonspatial, minimum density optimisation routine finds that a 61% cull annum^{-1} is the most efficient way to meet the goal. This translates into approximately 14 900 horses culled (Fig. 9b) for $\sim$AU\$80 000 less than the non-optimised scenario.

Nonspatial vs. spatial optimisation for a constrained budget in a single district

We considered the South Alligator district again and an overall budget of AU\$2 million over 10 years (i.e. AU\$200 000 year^{-1}). Invoking the nonspatial, budget optimisation budget routine shows that for the allocated budget (total cost actually = AU\$1·98 million, a near-75% reduction of pigs is achievable by culling 35% of the population annually (Fig. 10a). This scenario ended up culling $\sim$ 69 000 pigs at an

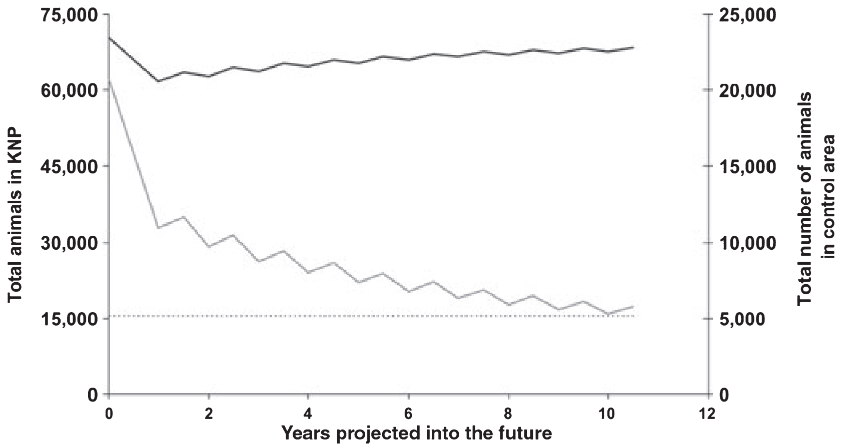

Fig. 8. Projections of feral horse numbers in the Mary River control area (grey line) and within the entire park (black line).

average cost of AU\$29 animal^{-1} and resulted in a 31% reduction in the park-wide pig population. Keeping all other parameters the same as in the previous scenario, but now invoking the spatial, budget optimisation routine (i.e. minimising the cost and area over which animals are culled), recommends a much higher culling rate (91% annually), giving 11 000 culled in the first year and ~ 1500 year^{-1} thereafter (Fig. 10b). The suggested culling area is substantially reduced, with only 14 of the original 53 cells (26%) being required to meet the 75% (or more) reduction target. Consequently, an efficient scenario might recommend killing fewer animals because overall densities are lowered for less money spent.

Nonspatial vs. spatial optimisation for a constrained budget park-wide

Running a scenario where only the park (and not the 10 km exterior buffer) is culled at 40% initially and 20% thereafter achieves a near-50% reduction for AU\$4·8 million, or approximately AU\$477 000 year^{-1} (total cull = 134 000 pigs). Using these same input parameters but setting the budget to AU\$4·8 million, and then invoking the Spatial/Budget optimisation routine predicts that a culling rate of 73% annum^{-1} for a total cull of 66 000 pigs (a little under half of those culled in the first scenario) could be achieved for AU\$4·8 million. This translates to AU\$72 pig^{-1} for a 78% park-wide reduction of pigs overall. Only 62 cells of the original 189 (32%) are needed to achieve the larger reduction resulting from the spatially optimised solution. The optimal spatial allocation based on reducing cost–benefit scores depends on the densities of pigs in each cell of the park and the priority listing derived from the damage and vexation layers. Furthermore, the optimal culling solution suggests that some boundary cells outside of the park be targeted to achieve a more efficient (in terms of cells and the number of cells targeted) culling rate than focusing on an uninformed, park-wide cull.

Discussion

The STAR model designed to optimise decisions for feral animal control in Kakadu National Park brings together most of the major biological, economic, spatial and temporal uncertainties of feral animal management into a single framework. The use of a spatially explicit lattice system, visualised in a commonly used spreadsheet program (Microsoft Excel®), allows for the emergent properties of relatively complex ecological dynamics and human interactions to be understood and used easily by managers and students of applied ecology. Furthermore, the ability to specify customised culling regimes provides a heuristic tool for the assessment of effectiveness and cost efficiency of various management choices.

The reliability of the STAR model scenario analysis is contingent on the level of understanding and quantification of the biological and ecological characteristics of the target species. Therefore, any 'mistakes' of assumption are measured in terms of the programmer's and scenario developer's time, rather than the failure of a scheme at the point of implementation (Macdonald & Rushton 2003). However, the models are only as good as the assumptions and data on which they are based (Conroy *et al.* 1995; Turner *et al.* 1995). For example, although we have information regarding the relative change in carrying capacity among habitat types, there is only limited information on the potential for these habitats to support a specified number of individuals. Estimating model output sensitivity to variation in input parameters demonstrates for specific species and management options the most important measurements to make during the adaptive management cycle (e.g. robust quantification of r_m for pigs in the example given). Also missing is specific information on the types of density-feedback processes that occur for each of the modelled species in this environment. For example, the choice of the growth response shape parameter (θ) will dictate to a large extent the capacity for these species to recover from extensive culling. Accurate data on animal dispersal patterns are also essential. The planning of optimal spatial culling regimes is contingent on quantifying a species' ability to move from high- (source) to low-density (sink) areas (Travis & Park 2004). However, at present the proportional values of dispersal supplied in STAR are based on logic rather than location- and species-specific data. If dispersal rates are in fact higher than those assumed, the importance of targeting the cells bordering specified culling areas becomes much higher than predicted by the model. Managers should therefore strive to census the within-park and adjacent populations stratified relative to habitat type, track

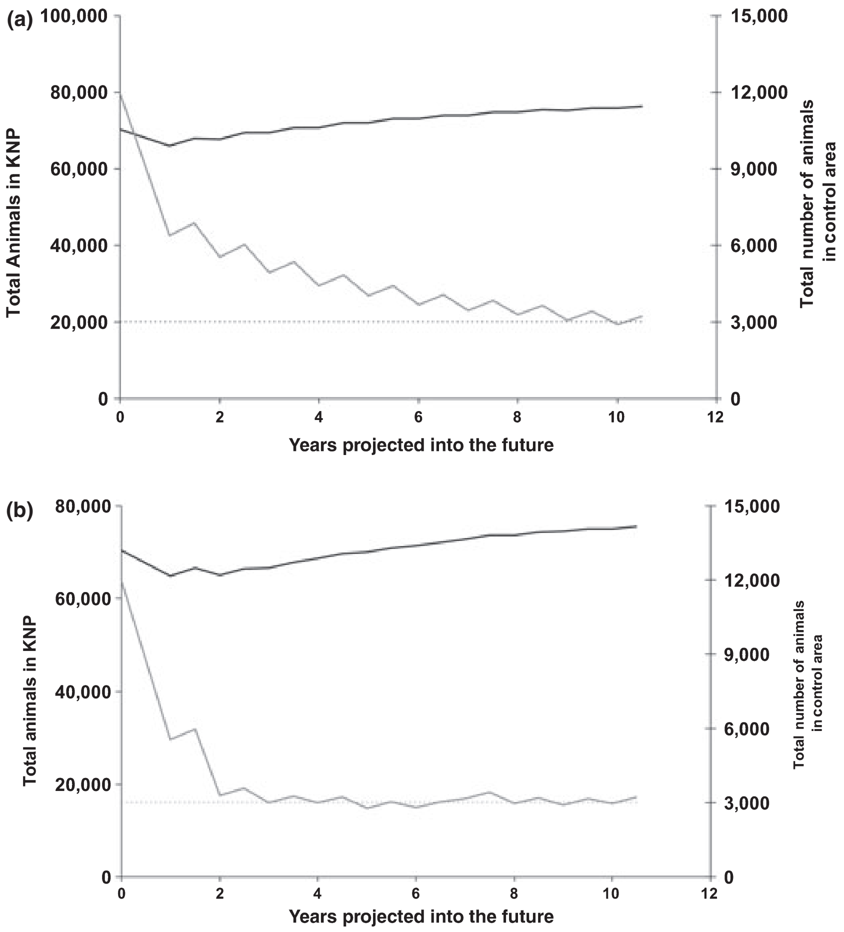

Fig. 9. Projections of the number of feral horses and in the South Alligator control area (grey line) and within the entire park (black line) using (a) a nonspatially optimised culling program with a constrained budget and (b) a spatially optimised culling strategy with a constrained budget.

individuals to determine movement rates, and monitoring population change over a range of densities (in time or space; e.g. McMahon *et al.* 2009). Regardless, we have provided realistic starting values based on analogous species or systems elsewhere and importantly, the capacity for these parameters to be updated (and their sensitivity tested) as new data are collected.

The scenario comparisons presented here highlight a critical component of feral animal control – avoiding offtakes that only serve to maximise rates of population increase (Bayliss & Yeomans 1989). If a cull is too low or not maintained, the program results in a steady offtake with little or no net effect on population density (Caughley 1985). STAR is therefore a practical tool that can help identify how to avoid this undesirable outcome, provided sufficient resources exist to implement a meaningful control target.

Although STAR is a deterministic model that does not account for variation in habitat-specific carrying capacities over time, this does not compromise its value. Scenario comparisons thus represent 'extreme' cases that can inform particular management pathways and test output sensitivities to variation in input parameters. This approach also encourages an adaptive management model whereby ongoing data collection is encouraged to update model inputs (Hauser, Pople, & Possingham 2006; McCarthy & Possingham 2007). We also deliberately chose to use a proportional harvesting scheme because it allows for maximum flexibility in a dedicated heuristic. Hence, the model can be applied to many situations where data on population size are often lacking. The optimisation routines are particularly powerful for determining the best way to allocate resources spatially and temporally. However, the successful use of the optimisation routines is contingent on an adequate assessment of the damage caused by these species and the current levels of vexation for management action implementation. Thus, a frequent effort to assess these parameters at the landscape scale is essential for the most effective management (Bradshaw *et al.* 2007).

Given the enormity of the feral animal problem in Kakadu National Park (Bradshaw *et al.* 2007) and the observation that many of the different species' populations overlap spatially and can interact (Corbett 1995), it might be more economically viable to target two or even three different species when planning an aerial shooting campaign. In this case, an opportunistic selection of target animals will occur within a specified culling area. Although STAR does not deal explicitly with this potential interaction, we do recommend using the model to design a culling program based on the species of highest management concern. Importantly, though there are no technical reasons why a multi-species optimisation routine could not be developed with further refinements. This is an important next step in the development of the model because when implementing a culling program, aerial shooters can destroy as many species as desired once detected. However, the danger is that too much

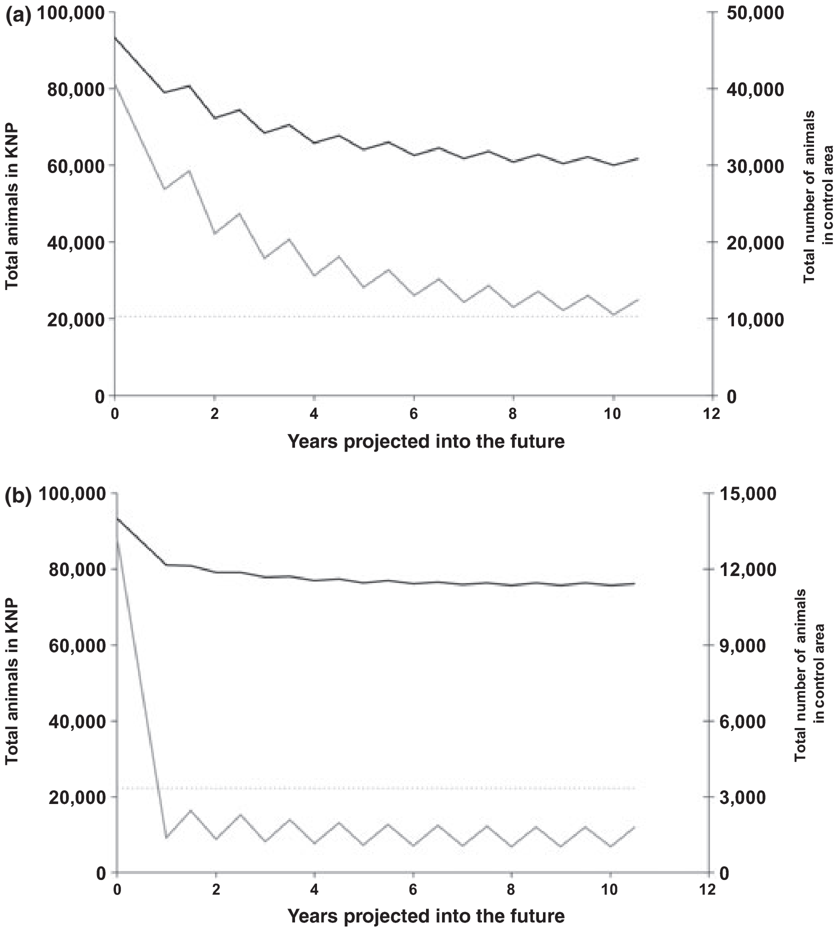

Fig. 10. Projections of feral pigs in the South Alligator control zone (grey line) and within the entire park (black line) using (a) a non-spatially optimised culling program and (b) a spatially optimised culling program.

effort will be wasted on detecting and destroying the species of secondary (or tertiary) concern, and reduce the project's overall capability of reaching the target within time and budget. Thus, we recommend that if a combination culling program is deemed appropriate, targeting the least important species should only occur if they do not detract excessively from the time required to identify and destroy the main target species.

The STAR model provides a user-friendly framework for managing feral animal densities that can be easily adapted to other situations because it is designed in an accessible and easily understood environment. This is possible because we envisage that the model and the VBA code will be freely available, for nonprofitable use. As such, the tool can also be readily applied in a teaching environment where inexperienced students can learn about landscape-scale modelling of animal management. Given that feral animals are a major cause of biodiversity loss (e.g. see Kingsford *et al.* 2009 for a recent overview), STAR makes an important contribution not only locally by providing Kakadu park managers with a custom-built tool, but to the broader conservation community because of its flexibility, adaptability and intuitive structure. A key feature of STAR is that there is a facility to update input information easily, thus making it a truly adaptive management tool where information such as age structure obtained during culls can be fed back into the model for more and more realistic projections and better land-use decisions (McCarthy & Possingham 2007).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. User manual for the Spatio-Temporal Animal Reduction (STAR) model.

Appendix S2. Visual Basic for Applications (VBA) code for subroutines in the Spatio-Temporal Animal Reduction (STAR) model.