Demography of feral camels in central Australia and its relevance to population control

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Abstract. Since their release over 100 years ago, camels have spread across central Australia and increased in number. Increasingly, they are being seen as a pest, with observed impacts from overgrazing and damage to infrastructure such as fences. Irregular aerial surveys since 1983 and an interview-based survey in 1966 suggest that camels have been increasing at close to their maximum rate. A comparison of three models of population growth fitted to these, albeit limited, data suggests that the Northern Territory population has indeed been growing at an annual exponential rate of $r = 0.074$, or 8% per year, with little evidence of a density-dependent brake. A stage-structured model using life history data from a central Australian camel population suggests that this rate approximates the theoretical maximum. Elasticity analysis indicates that adult survival is by far the biggest influence on rate of increase and that a 9% reduction in survival from 96% is needed to stop the population growing. In contrast, at least 70% of mature females need to be sterilised to have a similar effect. In a benign environment, a population of large mammals such as camels is expected to grow exponentially until close to carrying capacity. This will frustrate control programs, because an ever-increasing number of animals will need to be removed for zero growth the longer that culling or harvesting effort is delayed. A population projection for 2008 suggests ~10 500 animals need to be harvested across the Northern Territory. Current harvests are well short of this. The ability of commercial harvesting to control camel populations in central Australia will depend on the value of animals, access to animals and the presence of alternative species to harvest when camels are at low density.

Additional keywords: fertility control, harvesting, population dynamics.

Introduction

Camels (*Camelus dromedarius*) were introduced into Australia from the 1840s to the early 1900s for transport and hauling cargo in arid regions. Edwards *et al*. (2004) suggested that prior to 1920, the feral population of camels would have been small and scattered. However, by the 1930s, camels had become superseded by motor vehicles and rail for transport and consequently around 5000 captive camels were released between 1920 and 1941 (McKnight 1969; Edwards *et al*. 2004).

In 1966, McKnight (1969) estimated from interviews that there were between 15 000 and 20 000 wild camels in Australia; 4500 to 6000 of these in the Northern Territory. Between 1983 and 2001, aerial surveys (Graham *et al*. 1986; Short *et al*. 1988; Wurst and Saalfeld 1994; Edwards *et al*. 2004) indicated a population in the Northern Territory that was growing at ~10% per year; a rate that appears to have been maintained since the 1960s. Edwards *et al*. (2004) noted that this rate of increase approaches the maximum rate for camels, partly a result of the lack of natural predators in Australia, but also because food is

rarely limiting. They raised the concern that this near exponential rate of increase would continue unchecked for some time. Despite already having demonstrable impacts, wild camels have not been seen as a major pest by the wider community. The call is, thus, for present action to alleviate future costs (Edwards *et al*. 2008*b*).

Camels can have a detrimental impact on vegetation through overgrazing and, to a lesser extent, trampling (Edwards *et al*. 2008*a*). Other impacts of wild camels include competition with domestic stock, fouling of waterholes, destabilising of dune crests, damage to stock fences and social impacts such as damaging sites of cultural significance and being a motoring hazard (Edwards *et al*. 2004, 2008*a*). All of the above impacts are exacerbated, at least on a local scale, when camels form large herds.

The current and future size of these impacts will depend on the relationship between density and impact, the distribution of camels and the distribution of the environmental, economic and social 'assets' that are affected. The relationship between density and impact is unlikely to be linear, but is likely to vary spatially

and temporally. Following a review of studies of impacts of camels, Edwards *et al.* (2008*a*) recommended camels be controlled to broad-scale densities of 0.1–0.2 camels/km² to mitigate damage.

The three main options to control the impacts of camels include (Edwards *et al.* 2004; Saalfeld and Zeng 2008; Zeng and McGregor 2008):

(1) exclusion fencing;
(2) commercial harvesting including capture and domestication by landholders, resulting in the sale of camel products; and
(3) ground-based and aerial culling where camel products are not sold.

Fertility control is a further option (Hone 1992), but a species-specific method would need to be developed as would its broad-scale delivery (Lapidge *et al.* 2008). Given the life history of camels (i.e. high adult survival and low fecundity), control techniques will be most effective when they target adult survival.

However, the low densities, high mobility and low water requirements of camels will make their control difficult. Aerial shooting and trapping at water points has reduced the numbers of feral horses and donkeys in several areas of arid South Australia, Western Australia and the Northern Territory. In contrast to these species, camels form smaller herds and visit water points less frequently, reducing the effectiveness of these techniques. However, during drought, camels aggregate near water points and where there are remnant food supplies, which offers an opportunity for reducing numbers at a time when their impact is greatest. 'Judas' camels (Parkes *et al.* 1996; Edwards *et al.* 2004) could also be used to enhance culling and harvesting programs.

Commercial harvesting of camels may provide some reduction in population size, or at least a reduction in the rate of population growth. However, it will be economic to harvest camels only above a certain density and only in accessible areas. Throughout much of their distribution, camels exist at low densities (<2 camels/km², Edwards *et al.* 2004; Saalfeld and Edwards 2008) and much of their habitat is remote and difficult to access. Hence, their spatially variable and generally low density, combined with a punctuated, presently unpredictable pattern of ranging over large areas (Grigg *et al.* 1995; Edwards *et al.* 2001), makes harvesting difficult and costly. Increasing the value of camels and the availability of other species to harvest will make it more profitable to reduce camel populations to low densities and hold them there.

This study reassesses the growth of the Northern Territory camel population using population estimates presented by Edwards *et al.* (2004). In particular, population models other than exponential growth that incorporate density dependence should be considered. The theoretical maximum rate can be determined from an age structured model using life history data recorded by Dörges and Heucke (1995). These models can also be used to quantify the amount of control required to suppress growth either through harvesting, culling or fertility control.

Materials and methods

Unstructured and stage-structured temporal models were used to examine the impact of harvesting and fertility control on population size.

Unstructured models

It was not possible to determine *a priori* which model would provide the best fit to the time series data of camel abundance in the Northern Territory. Therefore, we chose to test three alternative models that were: (i) the exponential model (Eqn 1), (ii) the logistic model (Eqn 2) and (iii) the theta-logistic model (Eqn 3).

$$N_{t+1} = N_t e^{r_m} \tag{1}$$

$$N_{t+1} = N_t e^{r_m\left(1-\left(\frac{N_t}{K}\right)\right)} \tag{2}$$

$$N_{t+1} = N_t e^{r_m\left(1-\left(\frac{N_t}{K}\right)^{\theta}\right)} \tag{3}$$

Here, r_m is the maximum exponential rate of increase, N_t is population size at time t, K is carrying capacity and theta (θ) is a term influencing the strength of density dependence relative to K.

The exponential model characterises populations showing unbounded growth which might be representative of the dynamics of a camel population in the Northern Territory that is not close to carrying capacity. The logistic model might more closely represent the dynamics of a camel population that is approaching carrying capacity and the population's size is starting to asymptote and rate of increase is declining linearly with increasing density. The theta-logistic model would be favoured if the rate of increase of the population is a nonlinear function of density. If $\theta < 1$, density dependence is strong even when the population is far below carrying capacity. By contrast, if $\theta > 1$, density dependence is weak until the population is close to carrying capacity (Rockwood 2006).

Large mammals typically show most density-dependent changes in rate of increase at densities close to carrying capacity (Fowler 1981, 1987). In other words, density-independent limiting factors aside (i.e. a benign environment), population growth will tend to be exponential until close to carrying capacity (Fig. 1) when resources become limiting due to crowding. This pattern of population growth can be modelled using a theta-logistic (or generalised logistic) model (e.g. Eberhardt 1987), with greater values of theta indicating the increasing proximity of
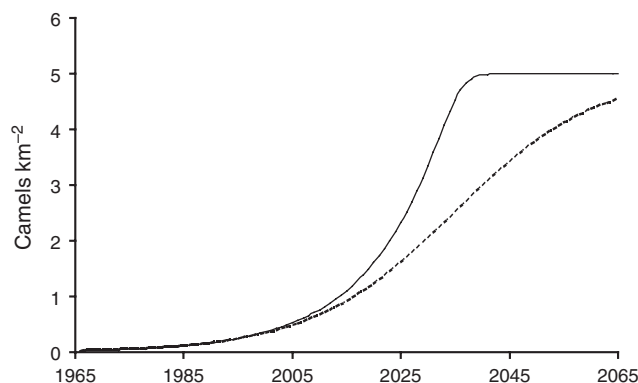

Fig. 1. Potential growth for the southern Northern Territory camel population according to the theta-logistic model when $\theta = 1$ (dashed line) and $\theta = 7$ (solid line). In both cases, K is arbitrarily set at 5 camels/km² and $r_m = 0.074$. Population density in 1966 is assumed to be 0.029 camels/km² (Edwards *et al.* 2004).

density to carrying capacity before density dependence becomes severe. When $\theta = 1$, the theta-logistic model is equivalent to the logistic model.

One use of this model is the calculation of the productivity of the population at various densities (Fig. 2). This is known as a yield curve, indicating the sustained harvest that can be taken from the modelled population while holding it at an equilibrium density (i.e. exponential rate of increase, $r = 0$) below carrying capacity. The maximum point of the yield curve is the maximum sustained yield (MSY). Assuming logistic growth, the MSY is at $0.5K$. Using the theta logistic model with $\theta > 1$, the MSY is pushed to the right (i.e. $>0.5K$). In both Figs 1, 2, theta has been arbitrarily set to 7, but is consistent with values used for other large mammals (Eberhardt 1987), and the value for K is also arbitrary apart from being greater than current population density.

Parameter estimation

Parameters for each model were estimated by maximum likelihood, assuming that observation errors followed a lognormal distribution (Hilborn and Mangel 1997). To estimate parameters for these models we used population estimates for camels in the southern Northern Territory ($\sim$259 000 km^2) reported by Edwards *et al.* (2004). The analysis also enabled us to revisit their estimates of current and historical rates of increase in that camel population. The observed data against which the models were fitted are presented in Table 1. A more conservative factor of 1.54 was used to correct population estimates for visibility bias for surveys before 2001 rather than 1.81 used by Edwards *et al.* (2004). This lower value represents the overall correction factor for the 2001 survey estimate.

Stage-structured model

Accurate projection matrices require detailed demographic data which are largely absent for camels in Australia. The most complete dataset was collected by Dörges and Heucke (1995), who studied a captive population in a large enclosure in central Australia.

Dörges and Heucke (1995) estimated that wild-living camels live to $\sim$30 years of age, but camels can live to 40 years of age (Carey and Judge 2001). We estimated that cohorts of age 31–40 make up about only 2% of the population, so have included these
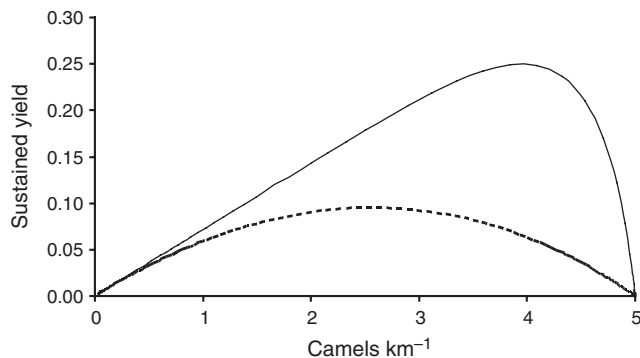
age classes in our analyses. They observed that camels bred all year round (but with a distinct increase in the frequency of births between June and November) and we have assumed that camels in central Australia are continuous breeders and that first breeding occurs at 5 years of age. The birth interval of most mature females was 22.2 months (1.85 years). However, females that lost a newborn were able to give birth after 14.4 months (1.2 years). To take this difference into account we used a weighted average birth interval of 19.9 months (1.66 years). Dörges and Heucke (1995) also noted that female fertility rate was 100%, but that 29% of newborns died soon after birth. They also estimated that camels older than 1 year had a survival rate of 96% per year. These estimates of reproductive output and survival come from the southern Northern Territory during the late 1980s and early 1990s. There is little scope to improve on these vital rates, so they should generate a rate of increase that is close to the maximum. To model these parameters, the projection interval was one year.

We used these estimates as initial values for the projection matrix transition probabilities. Final values for transition probabilities were derived by minimising the sum of squared errors between the size of the structured population and the best unstructured model (see below). The Microsoft Excel add-in 'Solver' was used to minimise the sum-of-squares.

The structured model comprised three stage classes: (i) yearlings, (ii) subadults (ages 1–5), and (iii) adults (ages 6–40), connected according to the life-cycle shown in Fig. 3 to describe the population dynamics.

Following the methods described by Caswell (2001), we used the following equations to calculate transition probabilities (P_i, G_i and F_i) for the projection matrix (Fig. 4):

$$P_i = \sigma_i(1 - \gamma_i) \tag{4}$$

$$G_1 = \sqrt{\sigma_1} \tag{5}$$

$$G_i = \sigma_i \gamma_i \tag{6}$$

$$F_2 = \sqrt{\sigma_1} G_2 \frac{m_2}{2} \tag{7}$$

$$F_3 = \sqrt{\sigma_1} \left(\frac{(1 + P_3)m_3}{2} \right) \tag{8}$$

where σ_i is the survival probability (one minus the ratio of deaths in stage i to the number of individual-years of exposure in stage i),

Fig. 2. Sustained yield (harvested camels/km^2) plotted against density (camels/km^2) for a theta-logistic model (solid line) of camel population growth with $\theta = 7$, $K = 5$ camels/km^2 and $r_m = 0.074$, and a logistic model (dashed line) with $K = 5$ camels/km^2 and $r_m = 0.074$.

Table 1. Estimated population size (or observed population size) of the feral camel population in the Northern Territory between 1966 and 2001
Estimates from 1983 (Short *et al.* 1988), 1984 (Graham *et al.* 1986), 1993 (Wurst and Saalfeld 1994) and 2001 (Edwards *et al.* 2004) are from aerial surveys and have been corrected for animals potentially missed by observers. The 1966 estimate is based on interviews with landholders (McKnight 1969). See Edwards *et al.* (2004) for details

Year	Uncorrected number	Corrected number	95% CI
1966	4500–6000	–	–
1983	11 600	17 864	±14 005
1984	23 549	36 265	±25 589
1993	33 000	50 820	±14 841
2001	52 329	80 533	±14 559

γ_i is the growth probability (and is equivalent to the reciprocal of the stage duration), m_i is the number of female births per female of stage i per year, P_i is the probability of surviving and remaining in the same stage, G_i is the probability of growing and surviving to the next stage and F_i is the reproductive output (births, m_i, multiplied by the probability of offspring survival). The term F_2 for reproductive output of subadults represents individuals that mature and reproduce during the projection interval. λ (the finite rate of increase, i.e. $\lambda = e^r$) was calculated as the dominant eigenvalue of the projection matrix.

Fertility control

Fertility control was modelled as a reduction in mean offspring production (m_i). The reduction was proportional to maximum offspring production and ranged from 90 to 10% of maximum offspring production in 20% decrements (Table 2). Fertility control only affected female camels and, for the purpose of this study, we did not include any compensatory increase in either offspring or sterile female survivorship, which has been observed in other vertebrates subjected to fertility control (Twigg *et al.* 2000; Saunders *et al.* 2002). Compensatory effects on ungulates following fertility control have previously been modelled as improvements in recruitment following reductions in population size (e.g. Hobbs *et al.* 2000), which is the expected density
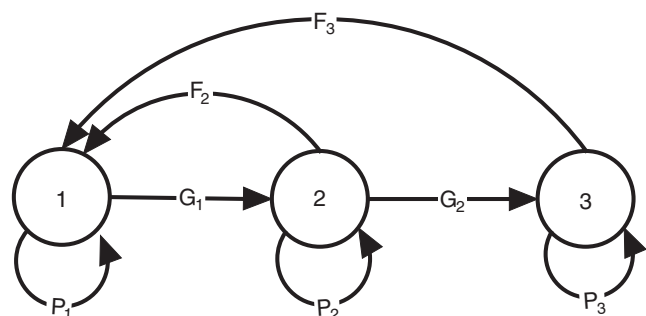
dependent response (Gaillard *et al.* 1998). The population growth that was modelled here was density independent.

Results

Unstructured models

The exponential growth model (Model 1) provided a good fit to the observed data (Fig. 5). The likelihood profiles for the two parameters of the model, initial population size (N_0) and r_m, indicate that the parameters could be estimated with reasonable confidence (Fig. 6; Table 3). We note that the estimated rate of increase is more correctly termed the maximum observed rate rather than the maximum rate. It is only our interpretation that labels it the latter.

The logistic growth model (Model 2) also provided a good fit to the observed data. The likelihood profiles revealed that N_0 and r_m could be estimated with confidence, but not carrying capacity K. The likelihood profile for K was 'flat' and an upper 95% confidence interval could not be calculated (at least not a biologically meaningful estimate) (Table 3).

The theta-logistic growth model (Model 3) also provided a good fit to the observed data. Again, N_0 and r_m could be estimated with reasonable precision, but not K and theta (Table 3).

Models were compared using second order information criteria (Table 4). Although all models provided a reasonable fit to the observed data, the exponential growth model (Model 1) provided the best approximation for the observed data (Table 4). This result supports the view that the feral camel population in the Northern Territory has been growing exponentially (Edwards *et al.* 2004), at least until 2001 when the

Fig. 3. Life-cycle corresponding to the projection matrix (Fig. 4). Stages are shown as circles. Stage 1 is yearlings, stage 2 is subadults (ages 1–5) and stage 3 is adults (ages 6–40).

Table 2.   The calculated reduction in mean offspring production (m_i) resulting from fertility control in stages $i = 2$ and 3

Percent remaining reproductive	m_2	m_3
100	0.202	0.236
90	0.182	0.212
70	0.141	0.165
50	0.101	0.118
30	0.061	0.071
10	0.020	0.024

$$\begin{bmatrix} P_1 & F_2 & F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{bmatrix}$$

Fig. 4. Projection matrix for a stage-classified feral camel population. G_i is the transition probability of moving from stage i to stage $i + 1$, P_i is the transition probability of surviving and remaining in the same stage and F_i is the stage-specific fertility. Because the duration of the yearling stage is the same as the projection interval, $P_1 = 0$.
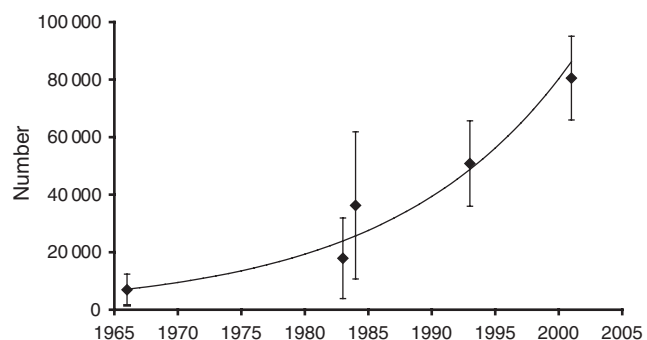

Fig. 5. Plot of camel abundance estimated from aerial surveys in Northern Territory (Short *et al.* 1988; Edwards *et al.* 2004), after correction for visibility bias. The fitted line is an exponential growth model (Model 1). Error bars represent 95% confidence intervals.
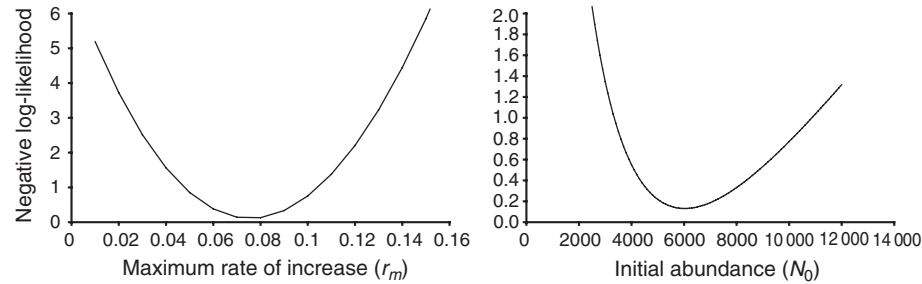
Fig. 6. Likelihood profiles for r_m and N_0 (Model 1).

Table 3. Fitted parameter values and 95% confidence intervals for three models of potential population growth fitted to data in Table 1

r_m, Maximum exponential rate of increase; N_0, initial population size; K, carrying capacity; θ, a parameter affecting the strength of density dependence relative to K

Model no.	Parameter	Value	Lower 95% CI	Upper 95% CI
1	r_m	0.074	0.04	0.12
	N_0	7122	2700	14 700
2	r_m	0.076	0.04	0.15
	N_0	7060	2800	19 400
	K	262 000	22 000	(undefined)
3	r_m	0.079	0.035	0.15
	N_0	7060	2600	18 000
	K	266 700	22 000	(undefined)
	θ	0.79	0.17	(undefined)

Table 4. Negative log-likelihoods and AICc for the 3 models

Most support is for the exponential growth model (Model 1). J is the number of parameters in the model, L_t is the minimised negative log-likelihood and AICc is the second order information criterion (Burnham and Anderson 1998)

Model no.	J	L_t	AICc
1	2	0.106	9.79
2	3	0.101	29.8
3	4	0.101	—[A]

[A]AICc could not be calculated for Model 3 because of the large number of parameters (J = 4) relative to the number of data points ($n = 5$).

last survey data were collected. Assuming that exponential growth has continued, the 2008 population size would be ~142 000 animals. Furthermore, there is currently no evidence from the aerial survey data that the feral camel population is approaching carrying capacity, nor can carrying capacity be estimated from the available data. A caveat to these results is that there are only five data points, so it is logical that the simplest model has been selected.

The estimate of r_m is almost identical to that estimated by Edwards *et al.* (2004) who also used a regression model, but fitted it using least-squares. A simple linear regression model of these data identifies N for 2001 and particularly N_0 as influential points as they are at the ends of the time series. Edwards *et al.* (2004) used a value of 5200 for N_0 based on McKnight's (1969) interview-based survey, but this value results in a poorer fit than the value estimated here. We included N_0 as a variable that needed to be estimated, since the starting value of the population was highly

uncertain. If population growth has been constant since 1966, then N_0 is likely to have been much higher than McKnight's (1969) estimate.

Stage-structured model

The initial transition probabilities derived from Dörges and Heucke (1995) produced the initial projection matrix **A**.

$$\mathbf{A} = \begin{bmatrix} 0 & 0.00974 & 0.245 \\ 0.843 & 0.768 & 0 \\ 0 & 0.192 & 0.933 \end{bmatrix}$$

Optimal parameter values for the projection matrix, derived by minimising the sum-of-squared differences between the population projection and the best unstructured model, produced the projection matrix **A′**.

$$\mathbf{A'} = \begin{bmatrix} 0 & 0.0169 & 0.196 \\ 0.848 & 0.791 & 0 \\ 0 & 0.198 & 0.961 \end{bmatrix}$$

Optimisation of the stage-specific vital rates (survival σ_I, growth γ_i, and births m_i) resulted in small changes in the transition probabilities, indicating that the original estimates (**A**) were close to the optimum values (Table 5). There were only small changes in survival probability, and the growth probabilities were fixed. Mean offspring production showed the largest changes.

The elasticity of λ to changes in P_i, G_i and F_i indicates that adult survival has the greatest influence on the rate of population change. The elasticity matrix (**E**) shows that subadult and adult growth and survival proportionally contribute 0.853 to λ, but juvenile growth and survival contributes only 0.0724 and fertility contributes a further 0.0704.

$$\mathbf{E} = \begin{bmatrix} 0 & 0.00341 & 0.0670 \\ 0.0724 & 0.202 & 0 \\ 0 & 0.0670 & 0.584 \end{bmatrix}$$

The stage-structured model indicates that λ for the population is 1.074 (i.e. $r = 0.071$), which is close to the value for λ derived from the best unstructured model (1.077). To stop the population growth, λ must be reduced below 1. Following Caswell (2001, eqn 9.110, p. 242), this could be achieved by a proportional reduction in adult survival of $-0.074/0.853 = -0.868$ (i.e. an 8.68% reduction), equivalent to a tripling of the natural mortality rate.

Table 5.   Initial and optimised values of stage-specific vital rates

σ_I is survival probability, γ_I is growth probability and m_i is the number of female births per female. Values for γ_1, γ_2 and γ_3 were fixed since they are age dependent

Parameter	Initial value	Fitted (optimised) value
σ_1	0.71	0.719
σ_2	0.9605	0.989
σ_3	0.9605	0.989
γ_1	1	1
γ_2	0.2	0.2
γ_3	0.0286	0.0286
m_1	0	0
m_2	0.0602	0.202
m_3	0.301	0.236

Fertility control

Fertility control will reduce the rate of population growth but, to prevent population increase, the proportion of reproductive females that must be sterilised needs to be at least 70% (Fig. 7). As quantified above, reducing the already low reproductive output of camels will only produce a modest reduction in rate of increase, certainly relative to a reduction in adult survival.

Discussion

Population dynamics

As expected from their large body size and compared with other mammals, camels have a particularly slow maximum population rate of increase of 7–8% per year, as determined by their vital rates. The actual rate is highly sensitive to the estimate of adult survival (e.g. 93% survival = 4% growth; 96% survival = 8% growth), highlighting the value of control methods targeting adult survival.

Historical survey data support a population trajectory for camels in the Northern Territory at close to this maximum rate, although the actual rate is sensitive to the initial, rough estimate in the 1960s. Despite the fact camels have occupied many areas of the southern Northern Territory for over 50 years, they do not appear to have reached carrying capacity where rate of increase would average zero over a large number of years. Edwards *et al.* (2004) estimated an annual exponential rate of increase of 0.093 (~10%) for the camel population between the two survey estimates of 1993 and 2001. Given the uncertainty in each of the density estimates, this rate of increase would have had a broad confidence interval and should not be extrapolated too far in time when more conservative estimates are available from a longer time series and from maximum rates based on camel demography.

The pattern of relatively slow population growth displayed by camels is an obvious advantage for control, with relatively few animals needing to be removed to keep $r \leq 0$. However, as can be seen from the yield curve (Fig. 2), an ever increasing number of animals are required to be removed to hold the population steady as density climbs almost to carrying capacity. In other words, the restraint on growth through density dependence provides little assistance for control of camel populations. This is not because camels are in a phase of establishment in central Australia (although that exacerbates the problem), but is a characteristic of established large mammal populations.

Impact of harvesting

To reduce population size it must obviously be harvested at a rate higher than it increases. To maintain a zero growth rate for the minimum estimate of the size of the 2001 Northern Territory camel population (80 533, Edwards *et al.* 2004) would require an annual harvest of ~6200 animals, assuming that the exponential rate of increase remains 0.074. To hold the projected 2008 population of 142 000 camels at zero growth would require an annual harvest of ~10 900 camels. However, this ignores spatial variation in both camel density and any potential harvest (see McLeod and Pople 2010 [this issue]), their unpredictable movement over large areas, and immigration from the broader national population (Saalfeld and Edwards 2008). The ability of harvesting to hold a population at a particular density will depend on the harvester's functional response, which describes how the consumption or offtake rate changes in response to changes in the density of prey (Holling 1959; McCallum 2000). In this case, the offtake from all harvesters is considered so it is more
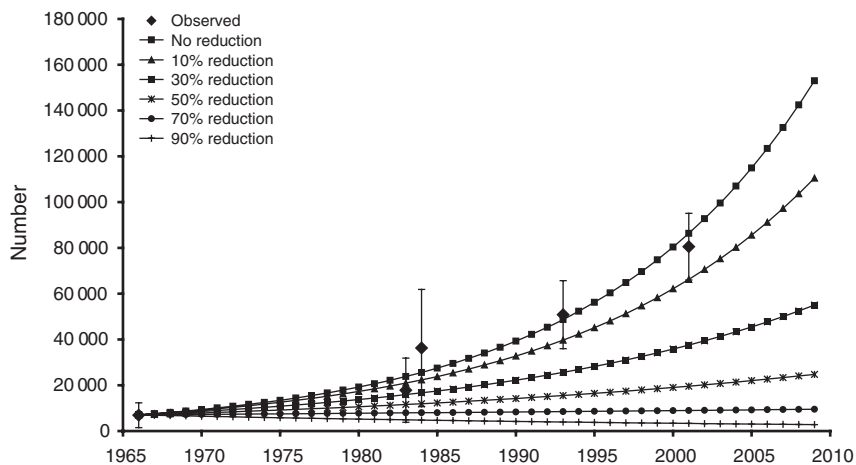

Fig. 7.   Reduction in population size realised by a range of fertility control programs that sterilise up to 90% of reproductive females.

appropriately termed the total response. Typically this function will reach an asymptote as there will be an upper limit to offtake dictated by factors such as numbers of harvesters, market availability and processing infrastructure. The latter two factors are equivalent to predator satiation. Conversely, at low densities, prey are difficult to find or it is simply not economically worth harvesting because of small returns.

Likely functional responses for camel harvesting are shown in Figs 8–10. These are hypothetical, as is the height of the sustained yield curve (determined here by an unknown K) and its skewness (determined here by a suggested θ). Currently, insufficient numbers of animals are being removed on a broad scale to stop the population from growing, and this is shown graphically in Fig. 8. Warfield and Tume (2000) reported a game meat harvest of 250–350 per year for the Northern Territory in the late 1990s, whereas Zeng and McGregor (2008) reported this live wild harvest across Australia to be 400–1000 per year for 2001–2008. Ramsay (1994) was unable to quantify the number field-shot for pet meat, but Zeng and McGregor (2008) reported a growing industry that in 2007 harvested 2700–3200 camels in Western Australia and 900–1400 animals in South Australia and the Northern Territory. In addition, an average of 250 camels were exported live from Australia over 1988–2007 (Zeng and McGregor 2008). This Australia-wide harvest of 5000–6000 per year represents less than 0.1% of the estimated population in 2007 of possibly one million camels (Saalfeld and Edwards 2008). Nevertheless, local reductions would be possible from these harvests.

Looking to the future, if the value of camels is increased, then offtake should also increase, all else being equal. There would then be the potential to suppress camel numbers to a low density. However, as shown in Fig. 9, above some moderate density, the population could still escape this 'predator pit' (Pech _et al._ 1995) and continue to grow to an equilibrium just short of carrying capacity. A further possible scenario is shown in Fig. 10. Here, it is economic to harvest camels at low density because harvesters have good access to them and the harvesters continue to operate because they have alternative and more abundant species (e.g. feral horses, donkeys and domestic cattle) to harvest. Nevertheless, commercial harvesting of feral goats has not lead
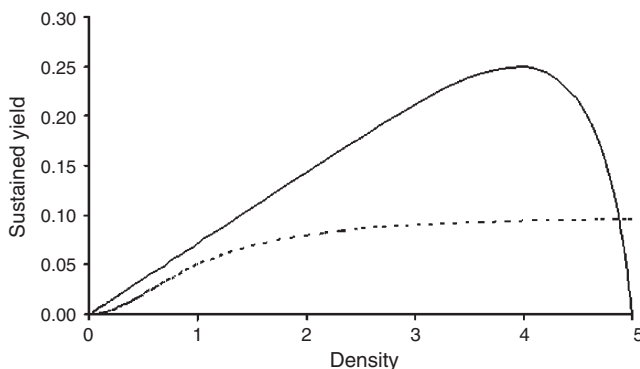
to suppression of populations to low numbers, despite their occurrence in less remote areas than camels and a substantial rise in their value in the mid-1990s (Parkes _et al._ 1996; Pople _et al._ 1996; A. R. Pople _et al._, unpubl. data). In contrast, camels have a much lower rate of increase increasing the chances of successful control.

Fertility control

Reducing the fertility of camels is likely to be a highly inefficient form of population control. Camels are widely dispersed in the Northern Territory and potential methods of contraceptive delivery, such as darting or food baiting, would be very expensive and logistically difficult to achieve on a broad scale. The elasticity analysis and age-structured modelling indicated that reducing fertility of females will result in only modest reductions in the rate
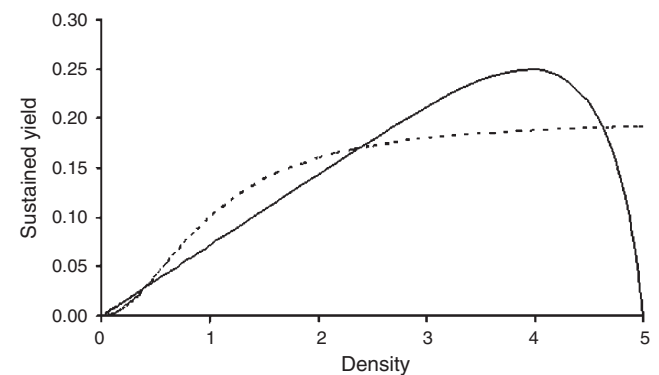

Fig. 9. Sustained yield curve (solid line) for a camel population (see Fig. 2) and a Type III functional response (dashed line) (Holling 1959) for their harvest. In contrast to the functional response shown in Fig. 8, the value of camel products has been increased allowing a higher harvest at low densities. Below ~2 camels/km^2, population growth is suppressed by harvesting to a density below 1 camel/km^2. If the population is above ~2.5 camels/km^2, the population continues to grow to an equilibrium at relatively high density just short of carrying capacity.
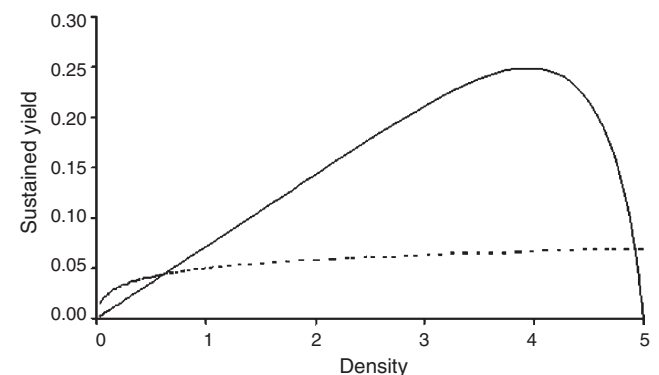

Fig. 10. Sustained yield curve (solid line) for a camel population (see Fig. 2) and a Type II functional response (dashed line) (Holling 1959) for their harvest. In contrast to the functional response shown in Fig. 8, alternative species are available for harvest allowing the camel harvest to continue at low camel densities. In contrast to Figs 8, 9, the population can be harvested to very low density or even to local extinction, as there is no low density refuge and so the response is convex (cf. sigmoidal) throughout.

Fig. 8. Sustained yield curve (solid line) for a camel population (see Fig. 2) and a sigmoidal Type III functional response (dashed line) (Holling 1959) for their harvest. The population continues to grow to an equilibrium at relatively high density just short of carrying capacity.

of population increase unless high rates of infertility can be achieved. The required high (>50%) proportion of females sterilised to stem population growth is consistent with results for other modelled ungulate populations (see Hobbs *et al.* 2000).

Fertility control of wild camels in the Northern Territory is currently not a viable option for management on a broad scale and it is unlikely that the substantial technological hurdles will be overcome in the near future. The most effective method of long-term population reduction will rely on increasing mortality of adults.

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