

DESERT KNOWLEDGE CRC

Modelling options for
management of feral camels
in central Australia

SR McLeod
AR Pople

Report
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Australian Government



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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 However, by the 1930s, camels had become superseded by motor vehicles and rail for transport, and consequently around 5 000 captive camels were released between 1920 and 1941 (Edwards et al. 2004).

McKnight (1969) estimated from interviews that in 1966 there were 15 000 to 20 000 wild camels in Australia, with 4 500 to 6 000 in the Northern Territory. Aerial surveys (Short et al. 1988, Graham et al. 1986, Wurst and Saalfeld 1994, Edwards et al. 2004) conducted between 1983 and 2001 indicated a population in the Northern Territory that was growing at about 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. Wild camels already have demonstrable impacts, but are not seen currently as a major pest. The call is thus for present action to alleviate future costs.

Camels can have a detrimental impact on vegetation through overgrazing and, to a lesser extent, trampling. There are a number of distinct potential impacts:

- The establishment of a herbivore in a new environment will invariably lead to a reduction in vegetation biomass and possibly to a shift in the vegetation to a new state. This has been observed for other, erupting ungulate populations (Klein 1968, Caughley 1976). Detecting changes in average vegetation biomass and state can be difficult in arid environments where vegetation biomass and composition fluctuate greatly. A further difficulty is in ascribing any impact to camels under environmental stochasticity and in the presence of grazing by other herbivores, particularly cattle.
- Certain plant species may be more heavily browsed by camels and if they are threatened or rare but considered valuable for other reasons, then the impact from camel grazing is quite specific.
- Attempts to rehabilitate vegetation, which is distinct from stopping land degradation, can be impeded by camel browsing.

Other impacts of wild camels include fouling of waterholes, destabilising of dune crests, damage to stock fences, and being a motoring hazard (Edwards et al. 2004). 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 ‘assets’ (i.e. vulnerable vegetation, heavily trafficked roads) that are affected. The relationship between density and impact is unlikely to be linear and is likely to vary spatially. Some researchers have suggested thresholds of density below which impacts are minor. Döriges and Heucke (2003) reported severe impacts on vegetation in south-western Northern Territory when camel densities were $> 2/\text{km}^2$. However, during drought, impacts would occur at lower densities, leading to a recommendation of sustainable densities of $0.2\text{--}1/\text{km}^2$, varying with habitat type. In northern South Australia, severe impacts were observed at $1\text{ camel}/\text{km}^2$ leading to a target density in the area of $0.1\text{ camels}/\text{km}^2$ (Phil Gee 2008, SA Rural Solutions, pers. comm.).

The three main options for control of camels include (Edwards et al. 2004):

- exclusion fencing
- commercial harvesting, including capture and domestication by landholders
- ground-based and aerial culling.

‘Judas’ camels (Parkes et al. 1996) could be used to enhance culling and harvesting programs. Given the life history of camels (i.e. high adult survival and low fecundity), control techniques should target adult survival. However, the low densities, high mobility, and low water requirements of camels 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, offer an opportunity for reducing numbers at a time when their impact is greatest.

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 only be economic to harvest camels above a certain density and only in accessible areas. Throughout much of their distribution, camels exist at low densities (<2 animals/km², Edwards et al. 2004) 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), make harvesting difficult and costly. Increasing the value of camels and the availability of other species – such as feral horses, donkeys, and cattle – to harvest is likely to increase the chances of reducing and holding camel populations at low densities.

Over the past 100 years, camels have spread throughout arid Australia and use a range of land systems. Their broadscale relationship with habitat has not been examined, but a species distribution model (Guisan and Thuiller 2005) could have a number of uses in camel management. Importantly, identifying preferred habitats can help focus control efforts. Furthermore, as camel numbers continue to increase further expansion in the camel range is likely and knowledge of habitat preference will indicate likely habitats at risk of invasion.

Current broadscale distribution is known only as snapshots in time from infrequent aerial surveys. These surveys provide useful regional estimates of abundance, but at fine scales (e.g. $<10,000$ km²), density estimates are imprecise, leading to misleading distribution patterns and potentially misdirected management effort. As an example, two identical surveys a short time period (e.g. 1 year) apart can yield quite different patterns of distribution as only small numbers of camels are seen when both density and survey intensity are low. To overcome this problem, a spatial model linking habitat to density can be used to spatially interpolate the survey data.

The objectives of this study are to:

1. Determine the impact of harvesting on camel population dynamics. This includes a sensitivity analysis to determine the relative importance of age-specific mortality and fecundity to the rate of increase. Further, the study assessed the harvest required to reduce population increase rate to zero and to reduce populations to particular target densities.
2. Determine environmental predictors of camel distribution in the Northern Territory.
3. Identify areas in the Northern Territory where commercial harvesting is feasible and the resultant potential reduction in densities is possible.

To achieve these objectives we used models to examine strategies for managing wild camels in the Northern Territory.

Materials and methods

To examine the impact of harvesting and fertility control on population size we used unstructured and stage-structured temporal models. To identify environmental predictors of distribution and examine the effectiveness of commercial harvesting we used GIS-based spatial models.

Non-spatial models

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:

1. the exponential model (Eq. 1)
2. the logistic model (Eq. 2)
3. the theta-logistic model (Eq. 3).

$$N_{t+1} = N_t e^{r_m} \quad \text{Eq. 1}$$

$$N_{t+1} = N_t e^{r_m (1 - N_t/K)} \quad \text{Eq. 2}$$

$$N_{t+1} = N_t e^{r_m (1 - N_t/K)^\theta} \quad \text{Eq. 3}$$

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

The exponential model characterises populations showing unbounded growth, and 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 growth rate is starting to asymptote. The theta-logistic model would be favoured if the rate of increase of the population is a nonlinear function of density. If theta is less than 1, density dependence is strong even when the population is far below carrying capacity. By contrast, if theta is greater than 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 (Figure 1) when resources become limiting due to crowding. This is in contrast to logistic growth, where rate of increase declines linearly with increasing density. The pattern of population growth for large mammals 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 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 (Figure 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 Figure 1 and 2, theta has been arbitrarily set to 7, but is consistent with values used for other large mammals (Eberhardt 1987).

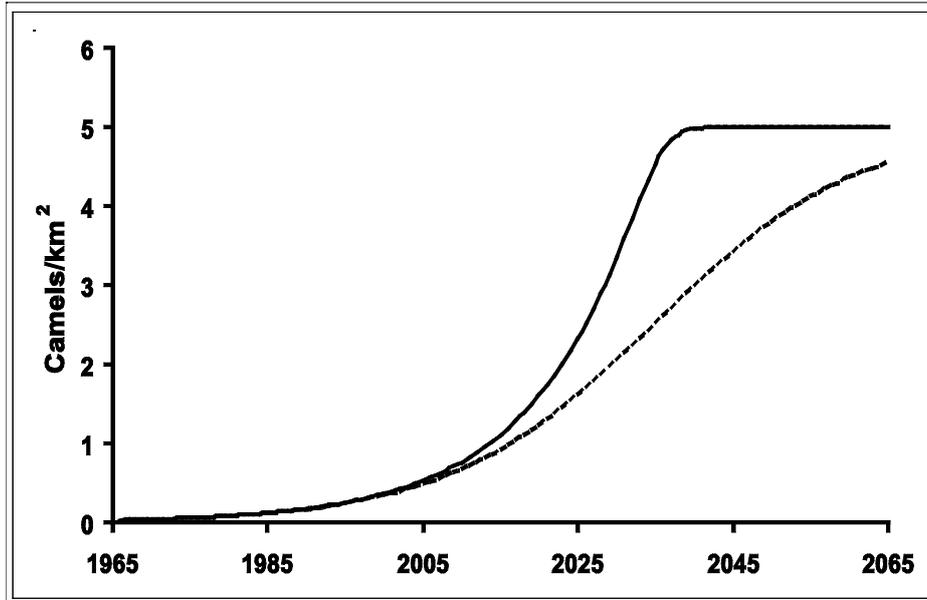


Figure 1: Potential growth for the Northern Territory camel population

Note: Figures is according to the theta-logistic model when $\theta = 1$ (dashed line) and $\theta = 7$ (solid line). In both cases, $K = 5$ camels/km² and $r_m = 0.074$. Population density in 1966 was assumed to be 0.029 camels/km² (Edwards et al. 2004).

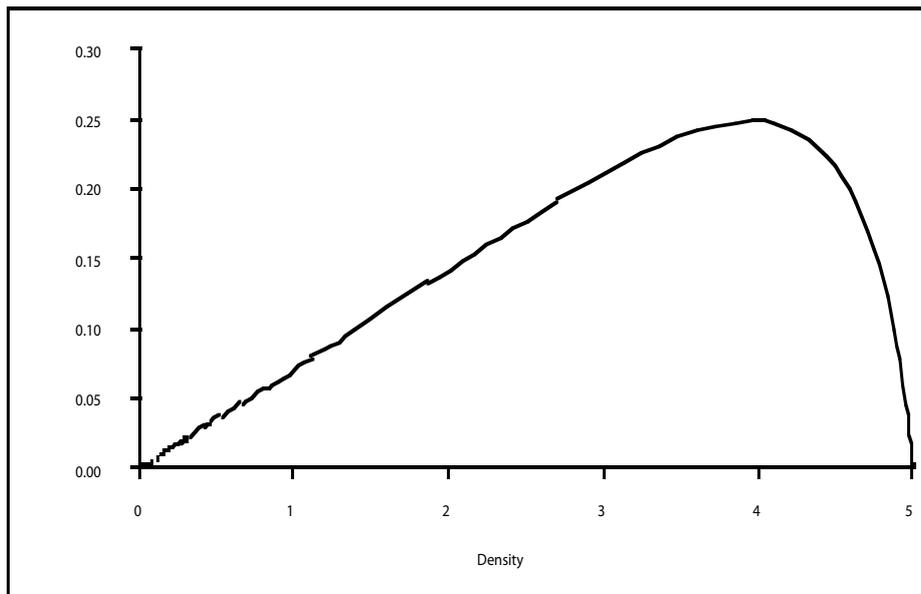


Figure 2: Sustained yield curve for a theta logistic model

Note: Figures is with $\theta = 7$, $K = 5$ camels/km² and $r_m = 0.074$.

Parameter estimation

Parameters for each model were estimated by maximum likelihood, assuming that observation errors followed a log-normal distribution (Hilborn and Mangel 1997). To estimate parameters for these models we used population estimates for camels in the southern Northern Territory 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.

Table 1: Estimated population size (or observed population size) of the feral camel population in the Northern Territory between 1966 and 2001

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	80 533	80 533	±14 559

Estimates from 1983 and 2001 are from aerial surveys and have been corrected for animals potentially missed by observers. The 1966 estimate is based on interviews with landholders. See Edwards et al. (2004) for details.

Stage-structured model

Accurate projection matrices require detailed demographic data which are largely absent for camels in Australia. The most complete data set was collected by Döriges and Heucke (1995), who studied a captive population in a large enclosure in central Australia. We derived initial values for survival probabilities and fecundities from their studies.

Döriges and Heucke (1995) estimated that wild-living camels live to about 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, and 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). Döriges 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 0.96 per year. These estimates of reproductive output and survival come from the southern Northern Territory during the late 1980s and early 1990s. To model these parameters, the projection interval was one year.

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

The structured model was divided into 3 stage classes:

1. yearlings
2. sub-adults (ages 1–5)
3. adults (ages 6–40)

and derived the following life-cycle graph (Figure 3) to describe the population dynamics.

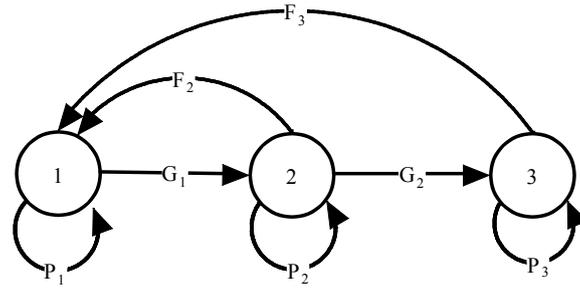


Figure 3: Life-cycle graph corresponding to the projection matrix (Figure 4)

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

$$P_i = \sigma_i (1 - \gamma_i)$$

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

$$G_i = \sigma_i \gamma_i$$

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

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

where σ_i is the survival probability (1 minus the ratio of deaths in stage i to the number of individual years of exposure in stage i); 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 juveniles represents individuals that mature and reproduce during the projection interval.

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

Figure 4: Projection matrix for a stage-classified feral camel population

Note: 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, $P_1 = 0$.

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 survivorship in either offspring or sterile female survivorship, which has been observed in other vertebrates subjected to fertility control (Saunders et al. 2002, Twigg et al. 2000).

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	0.2020	0.2360
90	0.1820	0.2120
70	0.1410	0.1650
50	0.1010	0.1180
30	0.0606	0.0708
10	0.0202	0.0236

Spatial models

Camel distribution and habitat preferences

The word ‘preferences’ is used here because it is familiar, but it is not entirely appropriate. In this project preferences refer merely to ‘associations’ as the analysis is only correlative and ‘choice’ cannot actually be determined.

Habitat preference was determined using two approaches. Firstly, preference for each vegetation community was calculated using a selection index (Manly et al. 2002), which is a simple measure that takes into account vegetation type and its availability. Secondly, the probability of habitat use was modelled using the selection index as a function of habitat covariates that were likely determinants of habitat selection.

Using a GIS we determined the vegetation community of the location where camels were observed in the aerial survey. Selection indices were calculated using camel number and vegetation community area. The selection index for vegetation type i was calculated as

$$w_i = \frac{O_i}{P_i} \quad \text{Eq. 4}$$

where w_i is the selection index for vegetation type i , O_i is the proportion of camels observed in vegetation type i , and P_i is the proportion of vegetation type i available in the environment.

Generalised linear models (GLMs) have been used to model the habitat preferences of a wide range of animals (Guisan and Zimmermann 2000). More recently generalised additive models (GAMs) have also been used to describe habitat preferences (Elith et al. 2006, Meynard and Quinn 2007). Generalised additive models are frequently more flexible than generalised linear models when the linear predictor can best be described as a sum of smooth functions of covariates using splines (Wood 2006).

In the current study we modelled camel habitat preferences and distribution using GAMs, specifically the `gam()` function from the `mgcv` package (Wood 2008) in the R statistical computing language (R Development Core Team 2008). Selection indices were used as the response variable along with a Gaussian error structure and an identity link.

The location and group size of camels were obtained from aerial survey data recorded by staff from the Department of Natural Resources, Environment, The Arts and Sport. Aerial surveys were conducted between August and October 2001. For details on survey methods see Edwards et al. (2004).

We imported the camel location (latitude and longitude) and group-size data into a GIS (Manifold System 8.0 Personal Edition, Build 8.0.9.0) and cross-referenced locations against habitat covariates. A list of covariates used in the analysis and their relationship to camel locations are given in Table 3.

Table 3: Covariates used to predict camel habitat preference

Covariate	Relationship to camel location	Source
Population centres	Nearest neighbour	Manifold < http://www.manifold.net >
Water sources (permanent and ephemeral)	Nearest neighbour	Manifold < http://www.manifold.net >
Major and minor roads	Nearest neighbour	Manifold < http://www.manifold.net >
Elevation (digital elevation model)	Point intersect	Jarvis et al. (2006) < http://srtm.csi.cgiar.org >
Aspect	Point intersect	Derived from digital elevation model
Slope	Point intersect	Derived from digital elevation model
Vegetation community	Point intersect	Wilson et al. (1990)

Nearest neighbour distance was calculated for human population centres, water sources, and roads. We hypothesised that camels might be attracted to water sources and avoid population centres and roads. For each camel location (a point from the aerial survey data) we determined points in the set of nearest neighbour covariates which were closest to each camel location. The nearest neighbour distance was recorded as the straight-line distance between the camel location and the closest point in the covariate set.

Using the vegetation classifications described by Wilson et al. (1990) we derived five simplified vegetation classes based on the dominant vegetation type in each community. The simplified classes were non-chenopod shrubland, grassland, chenopod shrubland, samphire shrubland, and bare.

Using the ‘Topology Overlay – Update’ function from the GIS, we determined the value of covariates (elevation, slope, aspect, and vegetation class) at each camel location. By overlaying the covariate data layer on the point locations, the value of the covariate at the intersection with each camel location was then recorded as a new attribute in the camel location data layer.

Figure 5 is a map of camel locations based on the aerial survey data. Figure 6, 7, and 8 are, respectively, the population centres, water sources, and roads in southern Northern Territory used in the analysis. Figure 9 is a map of the simplified vegetation classes based on the classifications of Wilson et al. (1990).

Predictions of the habitat preferences of camels were limited to vegetation communities for which we had data, based on the aerial survey location data. It would be meaningless to try to predict the habitat preference of camels for say, *Melaleuca* woodland, since there were no data from the aerial survey that included *Melaleuca* woodlands. Similarly, other vegetation communities, particularly in northern regions, could not be included in the analysis. The locations at which we predicted camel habitat preference are given in Figure 10, and at each point we determined the covariate values listed in Table 3.

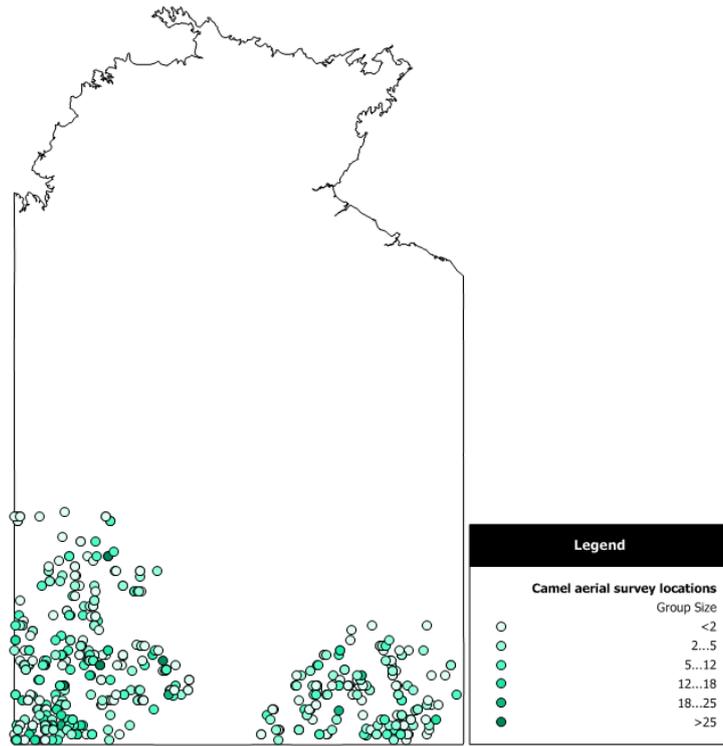


Figure 5: Camel locations recorded during aerial surveys of southern Northern Territory in August–October 2001

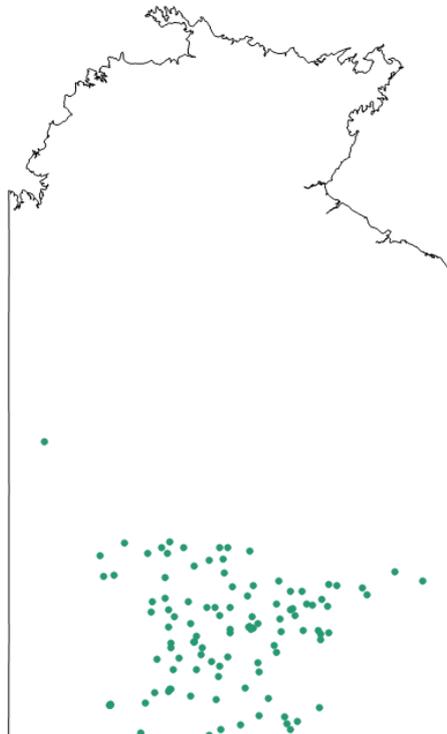


Figure 6: Southern Northern Territory human population centres

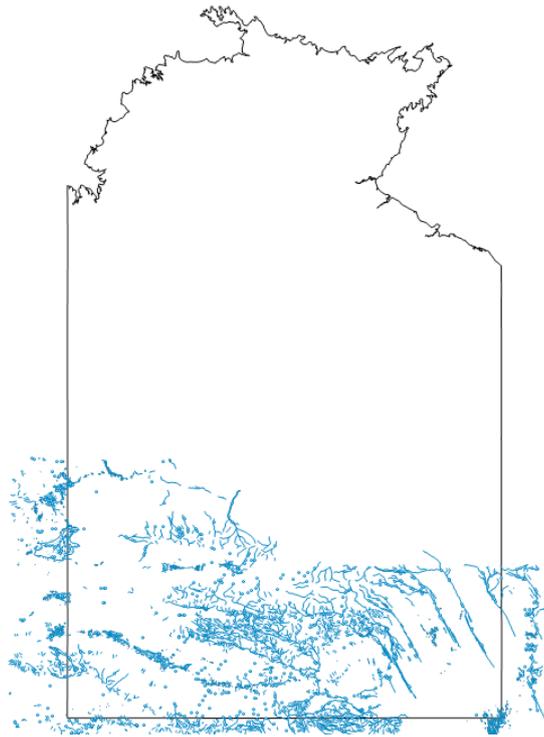


Figure 7: Hydrography (permanent and ephemeral water sources) in southern Northern Territory



Figure 8: Major and minor roads in southern Northern Territory

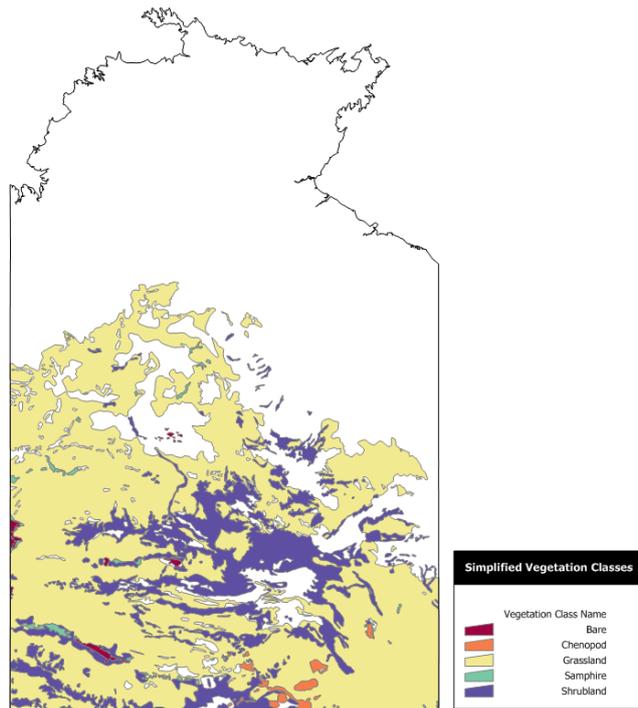


Figure 9: Simplified vegetation classes in southern Northern Territory within which camels were observed during the 2001 aerial survey

Note: Vegetation classes were based on Wilson et al. (1990)

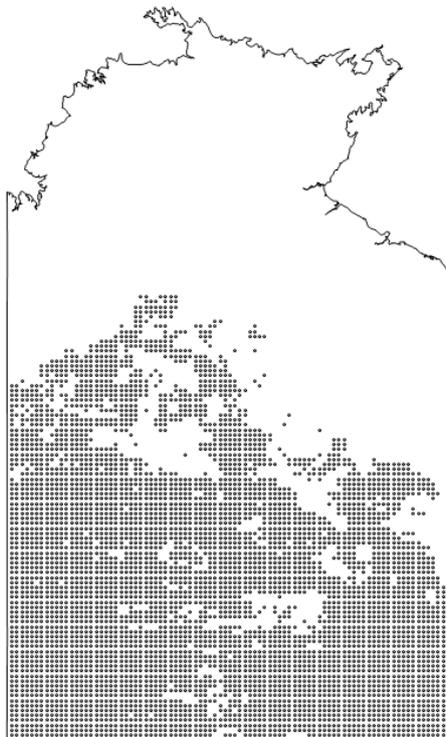


Figure 10: Point locations for which habitat covariate values were measured

Note: The covariate values were used in the predictive habitat model

The ‘best’ model was chosen by minimising GCV (Generalised Cross Validation) for all models. The GCV can be interpreted as an equivalent to AIC (Wood 2006). Using this model we determined the habitat association for each point in Figure 10. We used simple kriging to create a smooth surface of camel habitat preference. This surface is one estimate of the potential distribution of camels in southern Northern Territory.

Commercial harvesting

The cost of harvesting and the financial return from harvested animals will help determine which areas are likely to be suitable for commercial harvesting. We did not have access to data describing these costs or values so cannot provide a detailed analysis of commercial harvesting. As an alternative we determined which areas were likely to be suitable for live harvesting of camels based on the assumption that the most profitable form of commercial harvesting would be live capture for export. This analysis determines harvestable areas based on their distance from an existing road (see Figure 8). The analysis assumes that there is a strong relationship between areas that can be harvested profitably and distance from a major road. A similar pattern has been found for other commercially harvested wildlife species, such as kangaroos (Hacker et al. 2004).

We buffered the road network at set distances (25 km, 50 km, 100 km and 150 km) and assumed that areas within the buffered regions would be suitable for harvesting. Areas outside each buffered region were assumed to be unsuitable for harvest because harvesting costs will exceed the value of the harvested camels.

Results

Non-spatial models

Unstructured models

The exponential growth model (Model 1) provided a good fit to the observed data (Figure 11). The likelihood profiles for the two parameters of the model – initial population size (N_0) and maximum rate of increase (r_m) – indicate that the parameters could be estimated with reasonable confidence (Figure 12 and Table 4). It is worth noting 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.

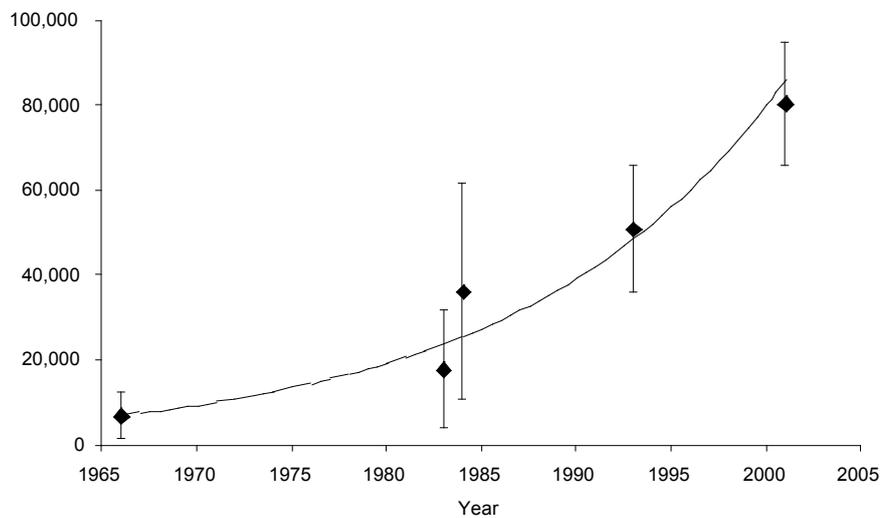


Figure 11: Model 1 – Exponential growth model plot of camel abundance estimated from aerial surveys in the NT

Note: Survey data from Short et al. (1988) and Edwards et al. (2004), corrected for visibility bias. The fitted line is an exponential growth model (Model 1). Error bars represent 95% confidence intervals.

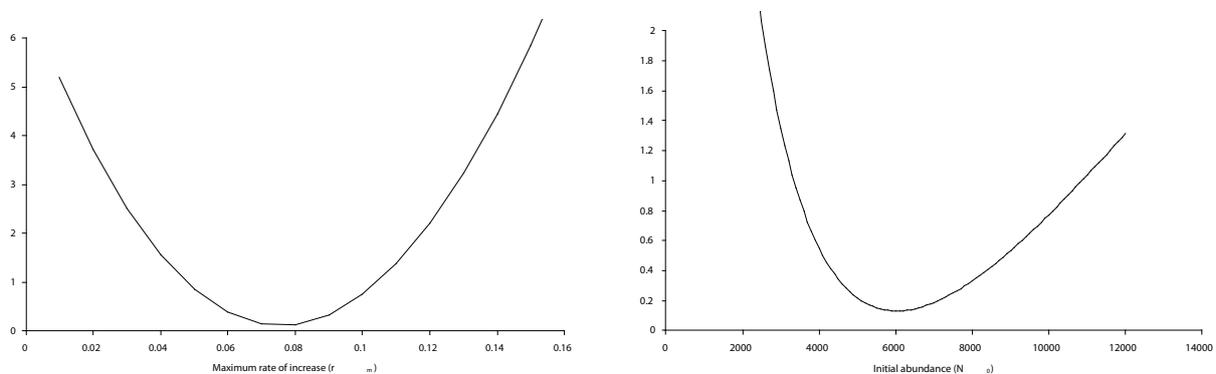


Figure 12: Likelihood profiles for r_m and N_0 (Model 1)

The logistic growth model (Model 2) also provided a good fit to the observed data (Figure 13). The likelihood profiles revealed that initial abundance (N_0) and the maximum rate of increase (r_m) could be estimated accurately, but that carrying capacity (K) could not. The likelihood profile for K was ‘flat’ and an upper 95% confidence interval could not be calculated (at least not a biologically meaningful estimate) (Figure 14 and Table 4).

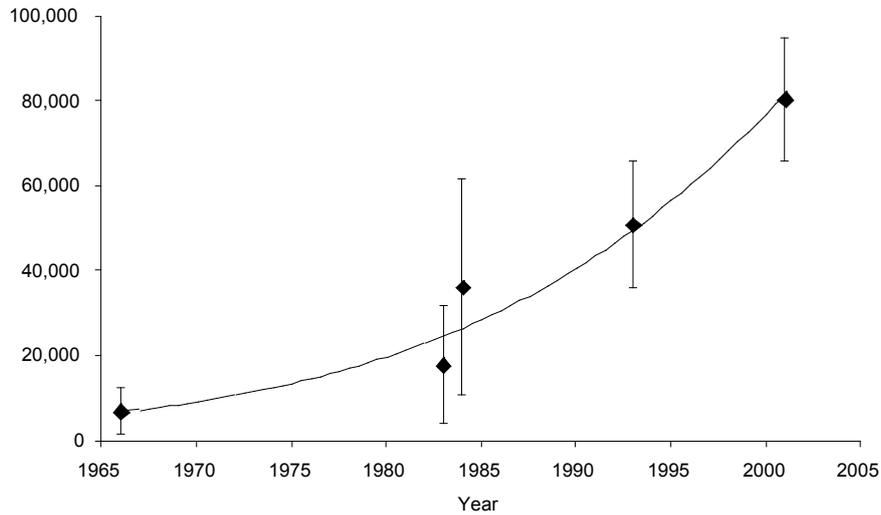


Figure 13: Model 2 – Logistic growth model plot of camel abundance estimated from aerial surveys in the NT

Note: Survey data from Short et al. (1988) and Edwards et al. (2004), corrected for visibility bias. The fitted line is a logistic growth model (Model 2). Error bars represent 95% confidence intervals.

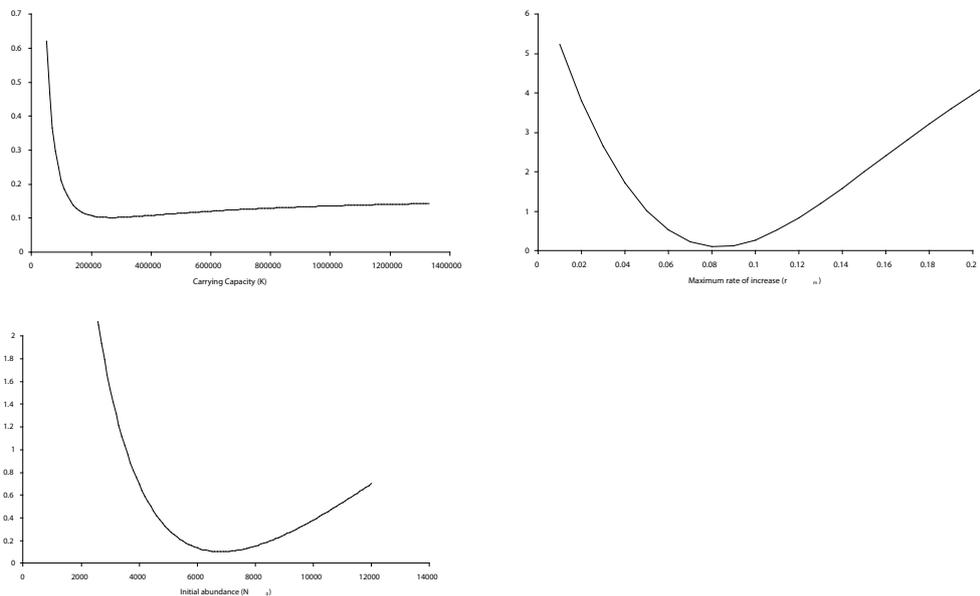


Figure 14: Likelihood profiles for a) carrying capacity (K), b) maximum rate of increase (r_m), and c) initial abundance (N_0)

The theta-logistic growth model (Model 3) also provided a good fit to the observed data (Figure 15). Again, initial abundance (N_0) and the maximum rate of increase (r_m) could be estimated with reasonable precision, but carrying capacity (K) and theta (θ) could not (Figure 16 and Table 4).

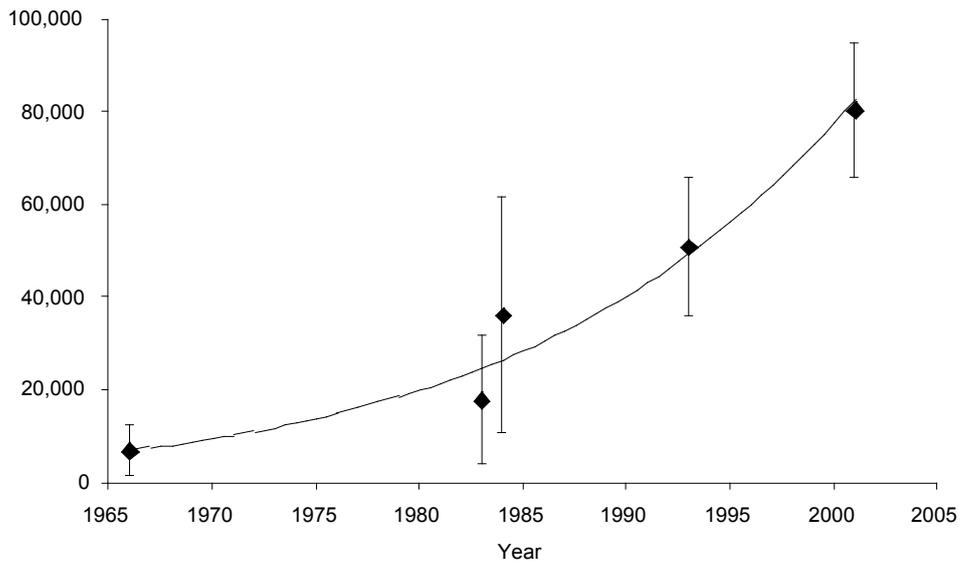


Figure 15: Model 3 – Theta-logistic growth model plot of camel abundance estimated from aerial surveys in NT

Note: Survey data from Short et al. (1988) and Edwards et al. (2004), corrected for visibility bias. The fitted line is a theta-logistic growth model (Model 3). Error bars represent 95% confidence intervals.

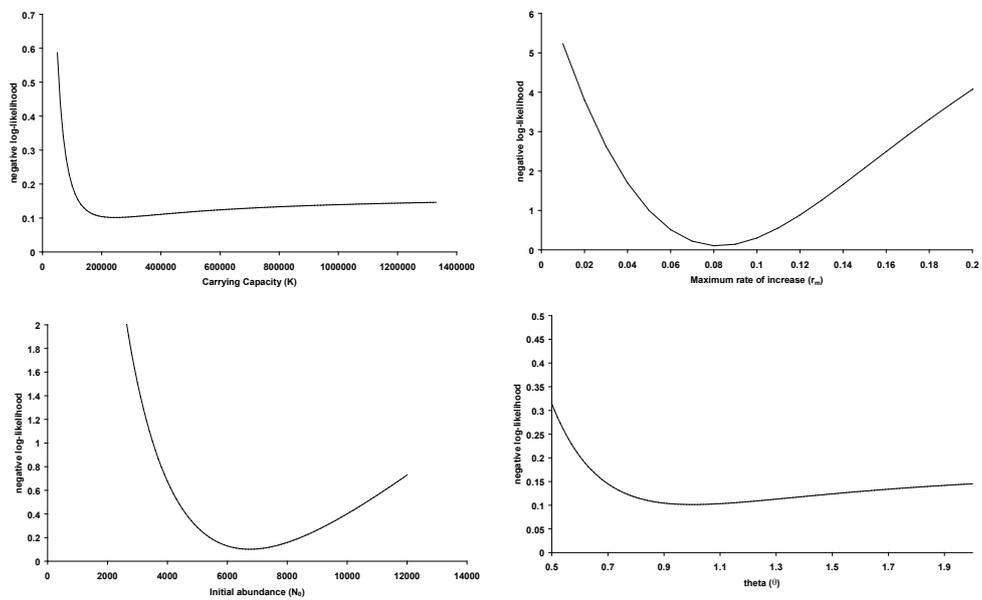


Figure 16: Likelihood profile for a) carrying capacity, b) maximum rate of increase (r_m), c) initial abundance (N_0), and d) theta (θ)

Table 4: Fitted parameter values and 95% confidence intervals for the three models

Model	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	2,600	18 000
	K	266 700	22 000	(undefined)
	θ	0.79	0.17	(undefined)

Models were compared using second order information criteria (Table 5). While 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 5). 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 last survey data were collected. Assuming that exponential growth has continued, the 2008 population size would be about 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 perhaps not surprising that the simplest model has been selected.

Table 5: Negative log-likelihoods and AICc for the 3 models

Model	K	L_t	AICc
1	2	0.106	9.79
2	3	0.101	29.80
3	4	0.101	.

Most support is for the exponential growth model (Model 1). K 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). [* AICc could not be calculated for Model 3 because of the large number of parameters (K = 4) relative to the number of data points (n = 5)].

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. Edwards et al. (2004) used a value of 5 200 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 unknown. If population growth has been constant since 1966, then N_0 is likely to have been much higher.

Stage-structured model

The initial transition probabilities derived from Döriges 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 were derived by minimising the sum-of-squared differences between the population projection and the best unstructured model, producing the projection matrix \mathbf{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 (\mathbf{A}) were close to the optimum values (Table 6). There were only small changes in survival probability, and the growth probabilities were fixed. Mean offspring production showed the largest changes.

Table 6: Initial and optimised values of stage-specific vital rates

Parameter	Initial value	Fitted (optimised) value
σ_1	0.7100	0.7190
σ_2	0.9605	0.9890
σ_3	0.9605	0.9890
γ_1	1.0000	1.0000
γ_2	0.2000	0.2000
γ_3	0.0286	0.0286
m_1	0.0000	0.0000
m_2	0.0602	0.2020
m_3	0.3010	0.2360

Note: Values for γ_1 , γ_2 , and γ_3 were fixed since they represent growth probabilities which are age dependent

The elasticity of λ (the finite rate of increase, i.e. $\lambda = e^r$) to changes in P_i , G_i and F_i indicate that adult growth and survival have the greatest influence on the rate of population change. The elasticity matrix (\mathbf{E}) indicates that adult growth and survival proportionally contributes 0.855 to λ , while juvenile growth and survival contributes 0.0724 and fertility contributes a further 0.0724. This result indicates that reductions in adult survival would have the greatest impact on λ .

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

The stage-structured model indicates that λ for the population is 1.074, 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. Using Caswell's (2001) eq. 9.110 (p. 242), this could be achieved by a proportional reduction in adult survival of $\frac{-0.074}{0.855} = -0.0865$ (i.e. an 8.65% reduction).

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% (Figure 17). Camels have a low rate of increase (7–8% per year) – a result of their high adult survivorship and low reproductive output – and reducing their already low reproductive output will only produce a modest reduction in rate of increase, certainly relative to a reduction in adult survival.

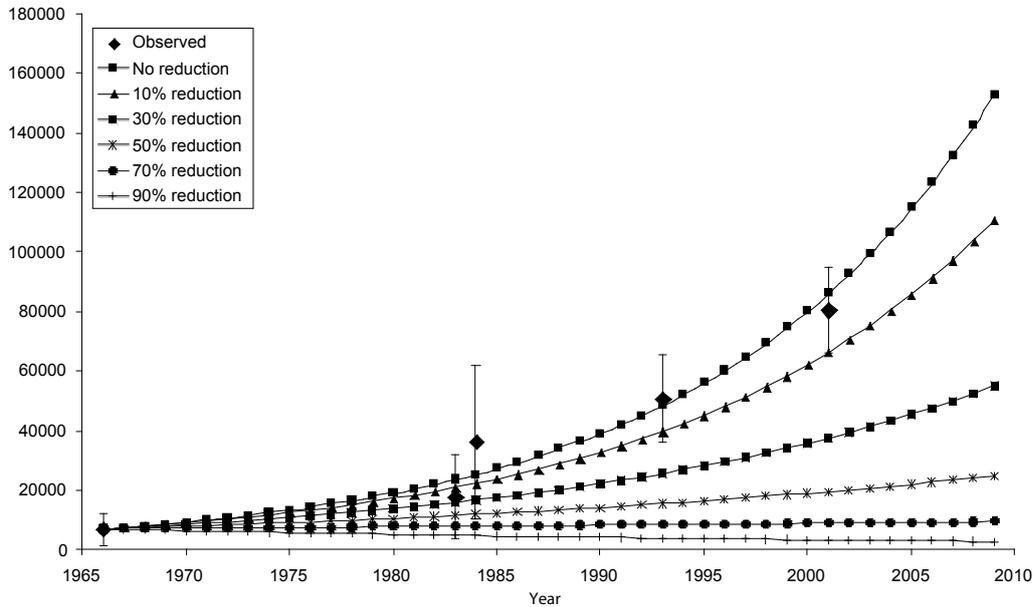


Figure 17: Reduction in population size realised by a range of fertility control programs that sterilise up to 90% of reproductive females

Spatial models

Camel distribution and habitat preferences

Selection indices greater than 1.0 indicate relative preference while indices below 1.0 indicate relative avoidance. The selection index relating camel density to vegetation community indicated that camels did not show a clear preference for one type of vegetation. Three vegetation classes had relatively high selection indices (Table 7). These vegetation communities include *Plectrachne melvillei* hummock grasslands (Mapping Unit 79), chenopod open-herblands (Mapping Unit 109), and *Acacia tetragonophylla* – *A. kempeana* sparse shrublands (Mapping Unit 73). Although greater numbers of camels were observed in hard spinifex hummock grasslands (*Triodia basedowii*), these grasslands are relatively common and widespread, which had the effect of reducing their selection indices.

Table 7: The estimated preference for vegetation communities shown by camels from the 2001 aerial survey in the southern NT

Vegetation class	Selection index	Standardised selection index	Number of camels	Area (km ²)	Map Unit
<i>Plectrache melvillei</i> (Spinifex) hummock grassland with <i>A. aneura</i> (Mulga), <i>A. kempeana</i> (Witchetty Bush) tall open shrubland overstorey	8.15	0.161	5	744	79
Chenopod open herbland with ephemeral open herb/grassland	5.89	0.116	7	1440	109
<i>A. tetragonophylla</i> (Dead Finish), <i>A. kempeana</i> (Witchetty Bush) sparse shrubland with herb/grassland understorey	5.58	0.110	45	9767	73
<i>Triodia basedowii</i> (Hard Spinifex) hummock grassland with <i>Allocasuarina decaisneana</i> (Desert Oak) low open woodland or <i>Acacia</i> tall sparse shrubland overstorey	3.36	0.066	18	6495	94
<i>A. kempeana</i> (Witchetty Bush) sparse shrubland to tall sparse shrubland with grassland understorey	3.11	0.061	7	2728	72
<i>Halosarcia</i> (Sapphire) low open shrubland fringing bare salt pans	2.88	0.057	10	4208	111
<i>E. gonylocarpa</i> (Marble Gum) open woodland with open hummock grassland understorey	2.55	0.050	7	3330	30
<i>Triodia basedowii</i> (Hard Spinifex) hummock grassland with <i>Allocasuarina decaisneana</i> (Desert Oak) open woodland overstorey between dunes	2.06	0.041	101	59 441	93
<i>Triodia basedowii</i> (Hard Spinifex) hummock grassland with <i>Acacia</i> tall sparse shrubland overstorey between dunes and <i>Zygochloa paradoxa</i> (Sandhill Cane Grass) open hummock grassland on dune crests	2.01	0.040	131	78 975	85
<i>Triodia spicata</i> (Spike Flowered Spinifex) hummock grassland with <i>Grevillea wickhamii</i> (Holly Grevillea), <i>Acacia</i> sparse shrubland overstorey	1.94	0.038	2	1249	78
<i>Atriplex vesicaria</i> (Bladder Saltbush) low sparse shrubland with ephemeral open herb/grassland	1.75	0.035	5	3456	110
Bare salt pan	1.73	0.034	4	2807	112
<i>Triodia pungens</i> (Soft Spinifex) or <i>Triodia basedowii</i> (Hard Spinifex) hummock grassland with <i>Acacia</i> tall sparse shrubland overstorey between dunes	1.52	0.030	28	22 395	86
<i>Triodia basedowii</i> hummock grassland with <i>A. aneura</i> (Mulga) tall sparse shrubland overstorey between dunes	1.34	0.026	15	13 572	82
<i>Triodia irritans</i> (Porcupine Grass) open hummock grassland	0.915	0.018	1	1325	90
<i>A. aneura</i> (Mulga) tall sparse shrubland with grassland understorey	0.881	0.017	11	15 132	71
<i>A. aneura</i> (Mulga) tall open shrubland with <i>Eragrostis eriopoda</i> (Woollybutt) open grassland understorey	0.876	0.017	29	40 141	65
<i>Triodia basedowii</i> (Hard Spinifex) hummock grassland with <i>E. gamophylla</i> (Blue Mallee) tall sparse shrubland overstorey	0.828	0.016	11	16 099	84
<i>A. aneura</i> (Mulga) tall sparse shrubland with <i>Cassia</i> , <i>Eremophila</i> (Fuchsia) low sparse shrubland understorey	0.676	0.013	3	5383	70

Vegetation class	Selection index	Standardised selection index	Number of camels	Area (km ²)	Map Unit
<i>Triodia basedowii</i> (Hard Spinifex) hummock grassland with <i>Acacia</i> tall sparse shrubland overstorey	0.665	0.013	11	20 051	81
<i>Triodia clelandii</i> (Weeping Spinifex) hummock grassland with mixed species low open woodland overstorey	0.389	0.008	3	9353	92
<i>E. microtheca</i> (Coolibah) low open woodland with open grassland understorey	0.381	0.008	4	12 714	27
<i>A. aneura</i> (Mulga)/mixed species low open woodland with open grassland understorey	0.281	0.006	2	8615	58
Complex of mixed species low open woodland between dunes with <i>Zygochloa paradoxa</i> (Sandhill Cane Grass) open hummock grassland on dune crests	0.244	0.005	1	4970	61
<i>A. estrophiolata</i> (Ironwood), <i>Atalaya hemiglauca</i> (Whitewood) low open woodland with open grassland understorey	0.206	0.004	2	11 794	59
<i>Triodia</i> (Spinifex) open hummock grassland with <i>A. aneura</i> tall sparse shrubland overstorey	0.169	0.003	1	7178	87
<i>Triodia pungens</i> (Soft Spinifex), <i>Plectrachne schinzii</i> (Curly Spinifex) hummock grassland with <i>Acacia</i> tall sparse shrubland overstorey	0.115	0.002	20	211 689	76
<i>Triodia basedowii</i> (Hard Spinifex) or <i>Triodia pungens</i> (Soft Spinifex) hummock grassland with <i>E. gamophylla</i> (Blue Mallee), <i>Acacia</i> tall sparse shrubland overstorey	0.0946	0.002	1	12 816	83

Note: The classification follows Wilson et al. (1990). Survey data is from Edwards et al. (2004). The table is sorted in order of preference determined by the selection index.

As indicated by the number of selection indices greater than 1.0, camels show a wide range of preferred vegetation communities. Camels showed a preference for half of the 28 vegetation communities represented in the sample. This result suggests that they may not have habitat requirements that are simply related to vegetation type. However, there appeared to be relative avoidance of vegetation communities that are classified as low open woodlands. These results also need to be interpreted cautiously since the camel population in the Northern Territory does not appear to be near carrying capacity. Relative preference for or avoidance of specific vegetation communities may be much clearer when the population is at or nearer to carrying capacity and so animals have been able to distribute themselves into all available habitat according to an 'ideal free distribution' (Fretwell and Lucas 1970).

Although vegetation community is an important variable of habitat choice by animals, habitat selection is frequently a function of many variables (Manly et al. 2002). The best model of camel habitat choice included position (latitude and longitude), elevation, and vegetation community. The best model had an adjusted $r^2 = 0.779$, explained 84.2% of the deviance, and had a GCV score = 0.00290. Other models which exclude one or more of the variables included in the best model had higher GCV scores. Model fit was judged to be adequate and there was no discernable pattern in the residuals (Appendix).

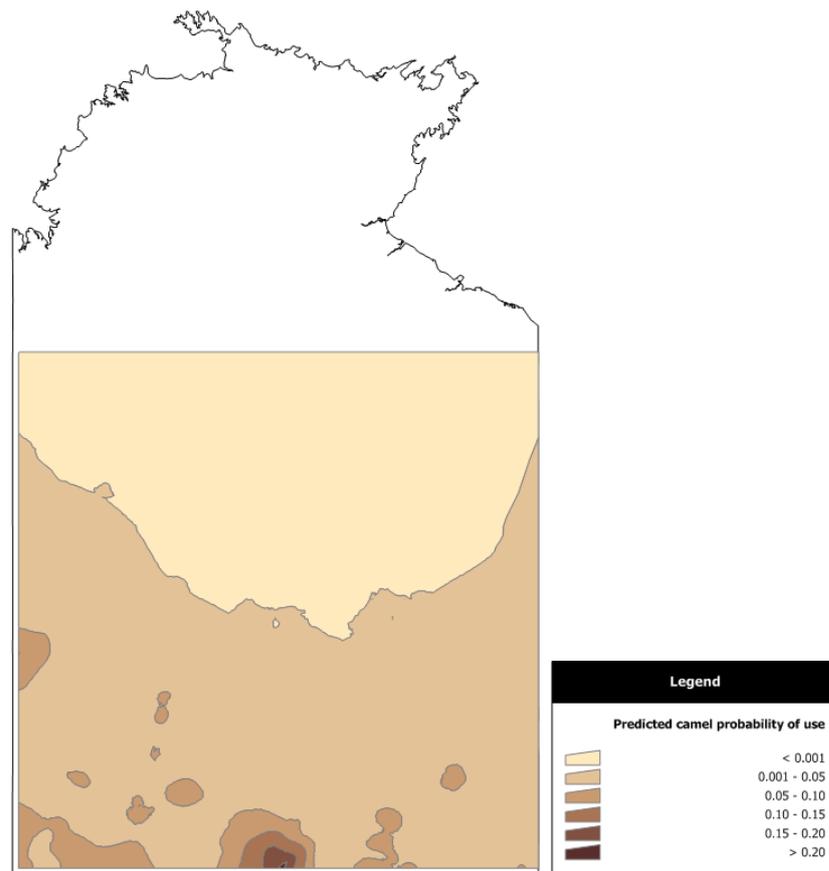


Figure 18: Predicted camel habitat preference in southern Northern Territory

Using the best model the predicted habitat preference surface (Figure 18) indicates that there are ‘hot spots’ of preferred camel habitat in the west and the south. These areas coincide with vegetation categories Map Unit 110 (*Atriplex vesicaria* (bladder saltbush) low sparse-shrubland with ephemeral open herb/grassland), Map Unit 73 (*Tetragonophylla* (Dead Finish), *A. kempeana* (Witchetty Bush) sparse shrubland with herb/grassland understorey), and Map Unit 82 (*Triodia basedowii* hummock grassland with *A. aneura* (Mulga) tall sparse shrubland overstorey between dunes).

However, the predicted habitat preferences do not always match the observed density of camels from the 2001 aerial survey (Figure 19). In particular, the high preference area in the south along the Northern Territory – South Australian border and in the west along the Northern Territory – Western Australia border were not observed in the aerial survey data.

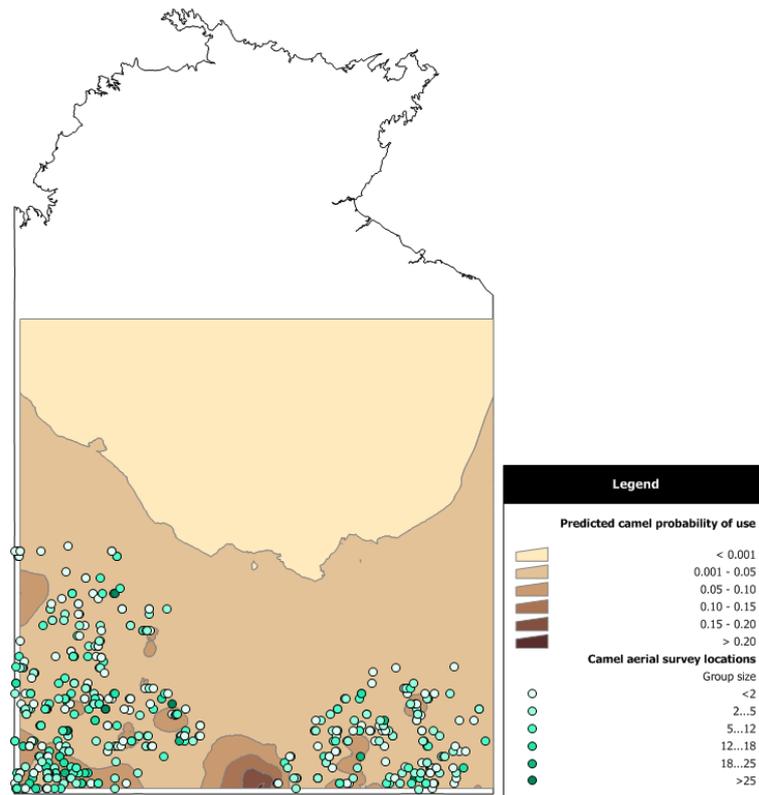


Figure 19: Predicted camel habitat preference and observed groups of camels based on the aerial survey data of 2001

Commercial harvesting

There are large regions in the south-west and west of southern Northern Territory that do not contain major or minor roads (Figure 20). These regions also coincide with predictions of highly preferred habitats for camels. Figure 21 indicates that if commercial harvesting only occurs within a 25 km buffer of major and minor roads there will be substantial areas in the west and south-east that are unsuitable for commercial harvesting. A 50 km buffer (Figure 22) still leaves large areas in the west and south-east that are unsuitable for commercial harvest. A 100 km buffer greatly reduces unsuitable areas in the west but still leaves a large area unsuitable for commercial harvesting in preferred habitats in the south-east (Figure 23). With a 150 km buffer (Figure 24) there is only a small area in the south-east that lies outside the harvest zone.

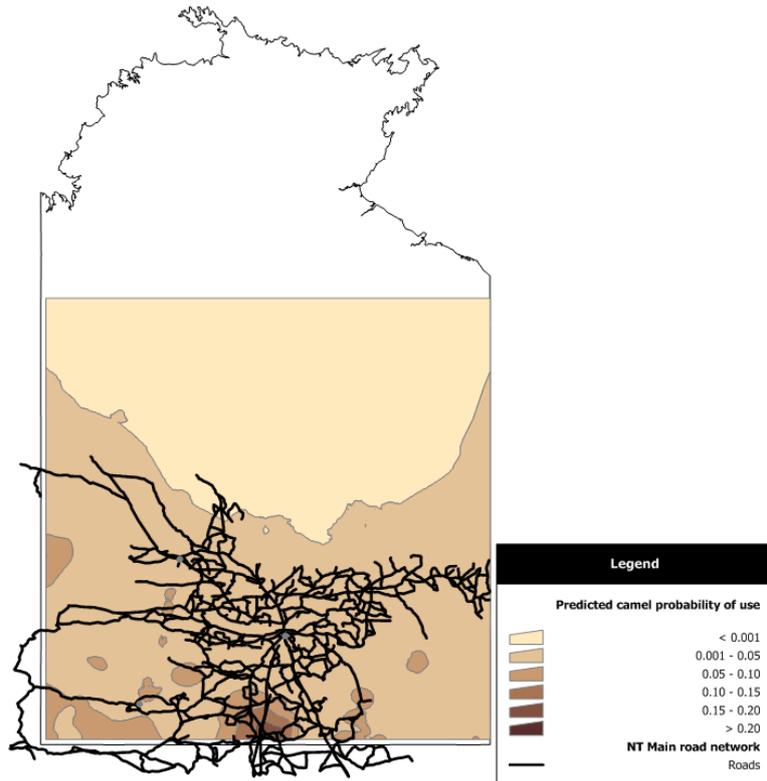


Figure 20: The road network of southern Northern Territory (Figure 8) laid over the map of habitat preference for camels (Figure 18)

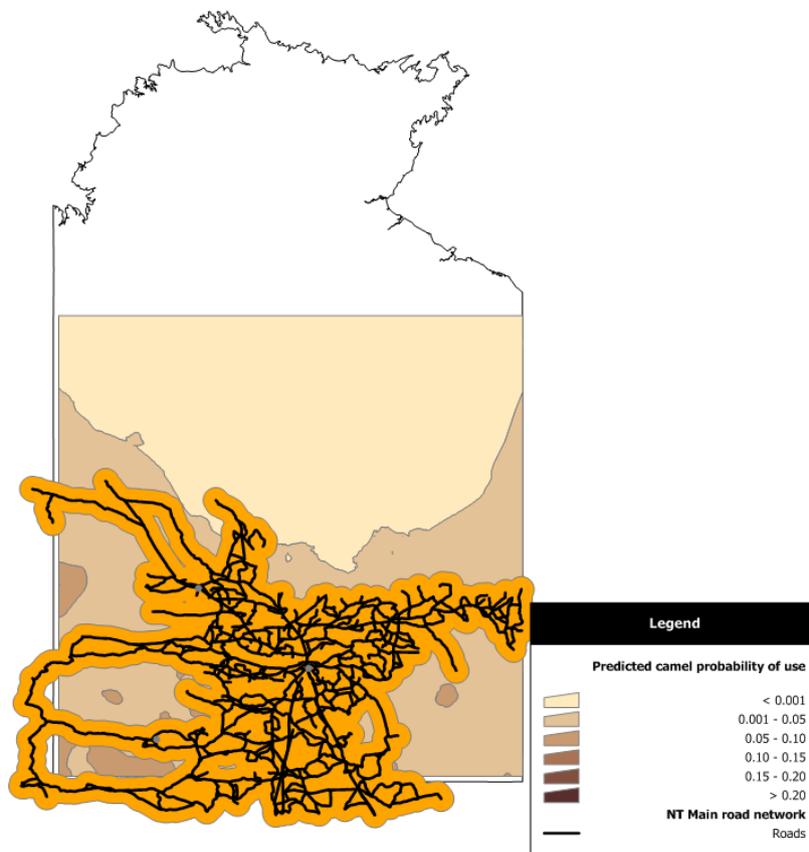


Figure 21: A 25 km buffer (orange) around the road network to indicate areas potentially suitable for commercial harvesting

Note: This is the road network of southern Northern Territory (Figure 8) laid over the map of habitat preference for camels (Figure 18).

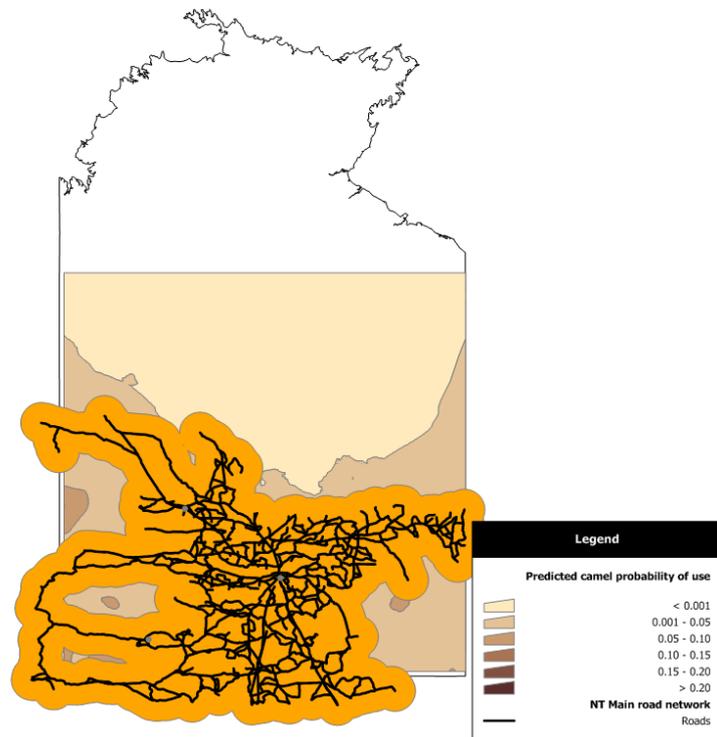


Figure 22: A 50 km buffer (orange) around the road network to indicate areas potentially suitable for commercial harvesting

Note: This is the road network of southern Northern Territory (Figure 8) laid over the map of habitat preference for camels (Figure 18).

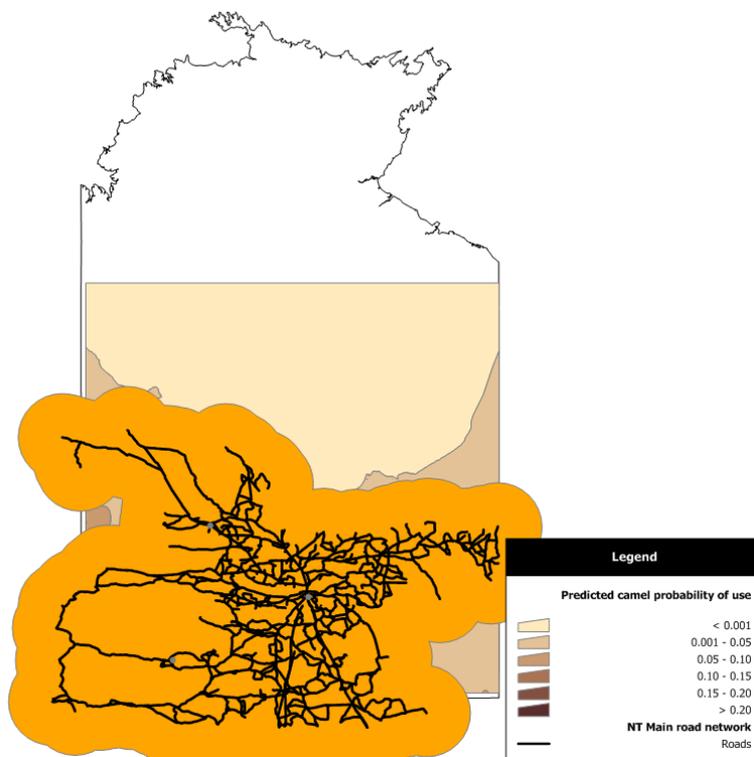


Figure 23: A 100 km buffer (orange) around the road network to indicate areas potentially suitable for commercial harvesting

Note: This is the road network of southern Northern Territory (Figure 8) laid over the map of habitat preference for camels (Figure 18).

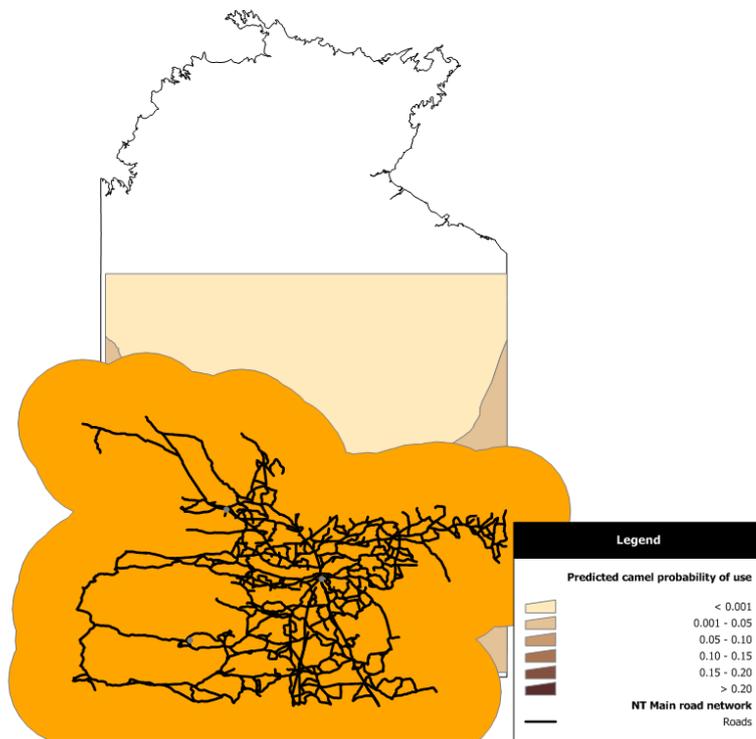


Figure 24: A 150 km buffer (orange) around the road network to indicate areas potentially suitable for commercial harvesting

Note: This is the road network of southern Northern Territory (Figure 8) laid over the map of habitat preference for camels (Figure 18).

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; 98% survival = 10% 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 that camels have occupied many areas of the southern Northern Territory for over fifty 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 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.

Theory and some empirical evidence predicts that a large mammal population will increase almost exponentially from low density up until close to carrying capacity, following a density-dependent reduction in firstly juvenile survival, then reproductive output, and eventually adult survival. For large mammals, as identified above, it is only when adult mortality is affected that there is a relatively substantial reduction in the population's growth rate.

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 (Figure 2), an ever-increasing number of animals are required to be removed to hold the population at a particular density below 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 ~5960 animals, assuming that the exponential rate of increase remains 0.074. A projection of population growth to the year 2008 predicts that the population size may have grown to about 142 000 camels. To hold this population at zero growth would require an annual harvest of about 10 500 camels. However, this ignores spatial variation in both camel density and any potential harvest (see below). 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). Typically, this function will reach an asymptote as there will be an upper limit to supply dictated by market availability and processing infrastructure. This is 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. As a result, the functional response takes a sigmoidal shape known as a Type III response. Without the 'refuge' from predators at low densities the functional response is convex throughout and known as a Type II response. If there is no asymptote at high densities, the response is a straight line and is known as a Type I response.

Likely functional responses for camel harvesting are shown in Figure 25–27. Currently, insufficient numbers of animals are being removed on a broad scale to stop the population from growing, and this is shown graphically in Figure 25. The caveat is that local reductions would be possible. 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 Figure 26, 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 Figure 27. 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.

The extent to which commercial harvesting can reduce camel populations requires further analysis. However, what is clear is that live capture is unlikely to be an effective form of population control in some areas of the west and most of the south-east of the NT. This is due to the large distances that harvesters will need to cover, the associated costs of finding, capturing and transporting camels to market, and the lack of suitable infrastructure in those areas. Unless the value of camels is very high and so offsets these costs, it is unlikely that commercial harvesting will be suitable for remote regions. However, in areas close to existing roads, commercial harvesting may be a useful adjunct to other forms of control.

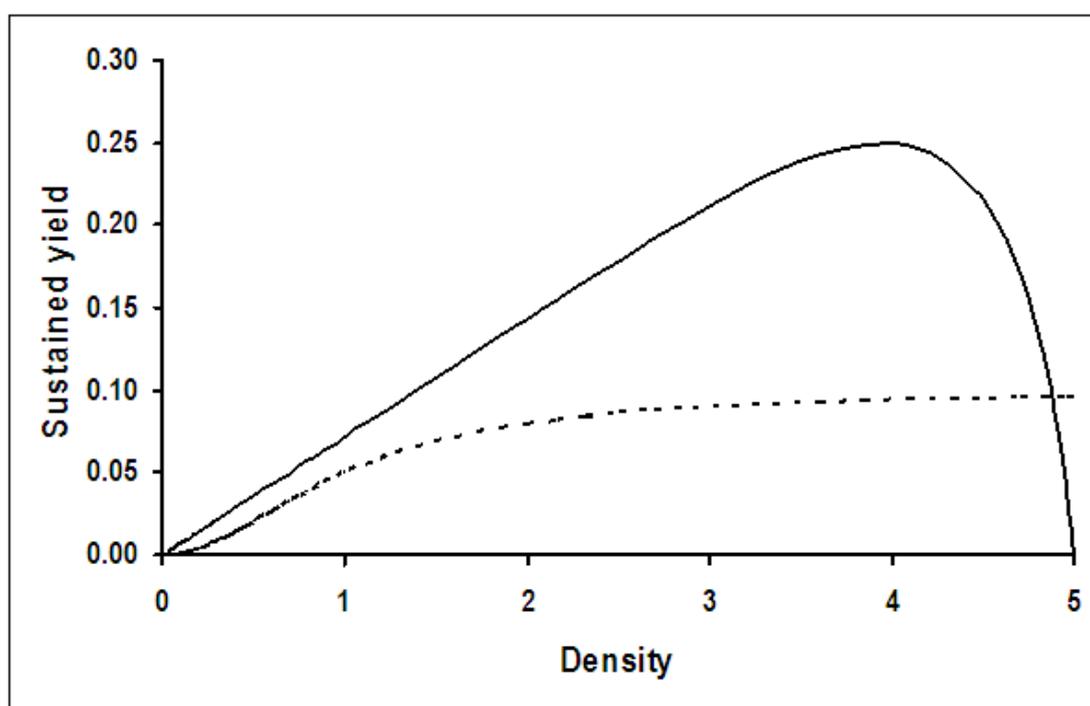


Figure 25: Sustained yield curve (solid line) for a camel population (see Figure 2) and a Type III functional response (dashed line) for their harvest

Note: The population continues to grow to an equilibrium at relatively high density just short of carrying capacity.

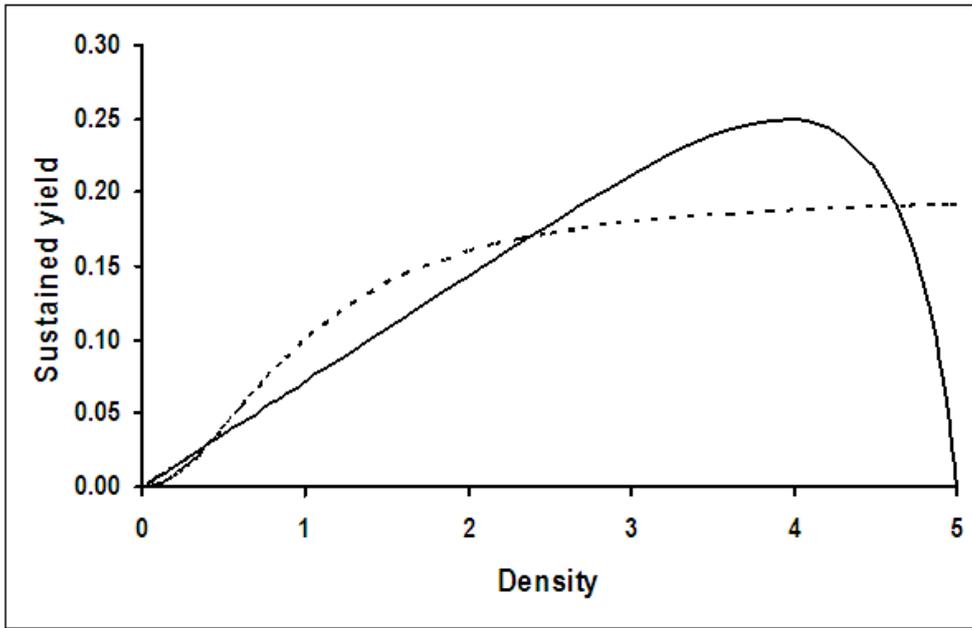


Figure 26: Sustained yield curve (solid line) for a camel population (see Figure 2) and a Type III functional response (dashed line) for their harvest – increased harvest value

Note: In contrast to the functional response shown in Figure 23, the value of camel products has been increased allowing a higher harvest at low densities. Below approximately 2 camels/km², population growth is suppressed by harvesting to a density below 1 camel/km². If the population is above approximately 2.5 camels/km², the population continues to grow to an equilibrium at relatively high density just short of carrying capacity.

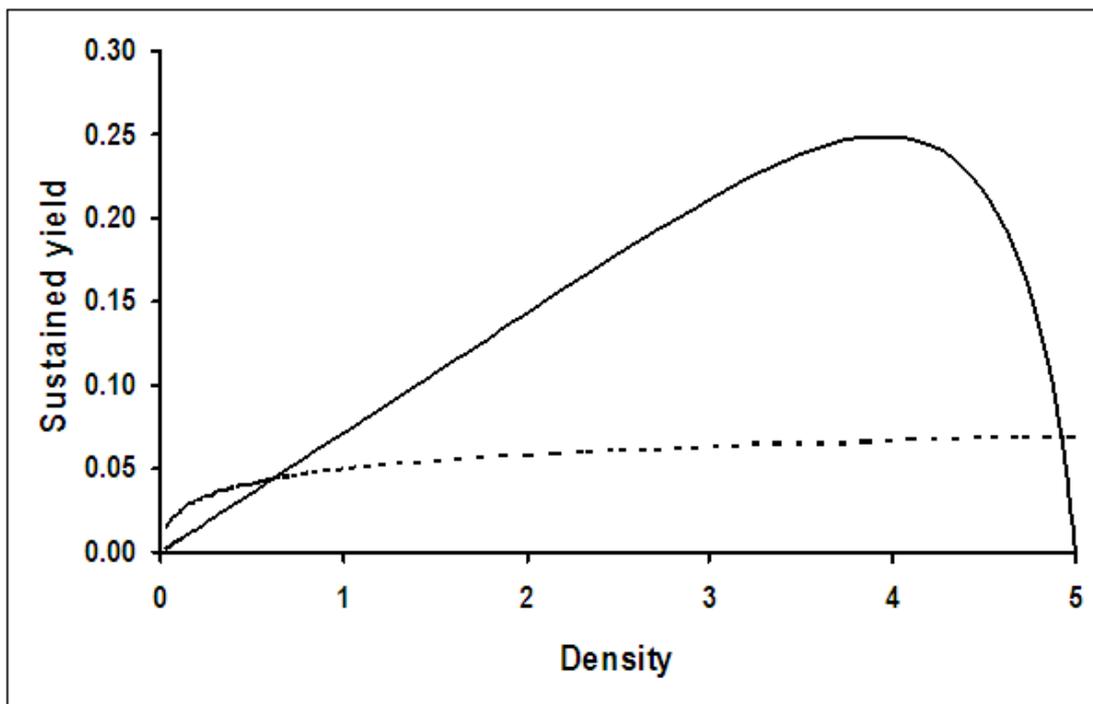


Figure 27: Sustained yield curve (solid line) for a camel population (see Figure 2) and a Type II functional response (dashed line) for their harvest – alternative species harvest possible

Note: In contrast to the functional response shown in Figure 23, alternative species are available for harvest allowing the camel harvest to continue at low camel densities. In contrast to Figures 23 and 24, the population can be harvested to very low density or even local extinction as there is no low density refuge.

Unfortunately, due to uncertainties in the costs of harvesting and the current value of camels we were unable to determine the potential reduction in camel density due to commercial harvesting. This remains a topic for future work.

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, will be very expensive. Furthermore, it is currently not technically feasible to deliver these contraceptives on a broad scale. The elasticity analysis indicated that reducing fertility of females will only result in modest reductions in the rate of population increase unless high rates of infertility can be achieved.

Fertility control of wild camels in the Northern Territory is not currently a viable option for broadscale management 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.

Distribution modelling

The predicted habitat preferences based on the aerial survey data from 2001 indicate that there are highly preferred areas in the south, west, and south-west. With the exception of the south-west region, these areas did not have very high numbers of camels in 2001. This could be due to error in the model, or, alternatively, low camel density and low sampling intensity have conspired to provide a deceptive picture of camel distribution. It would be very timely to conduct additional surveys to determine current camel density in specific habitats and validate this model.

Discrepancies between predicted habitat preferences and observed distribution may also be due to the fact that camels are not near carrying capacity in the Northern Territory. Camel populations are still growing at, or close to, their maximum rate and it may take many more years until equilibrium is reached between camel abundance and the environment. An additional survey of current camel distribution in the Northern Territory would indicate if camel distribution has changed in accordance with the predictions of the habitat preference model.

References

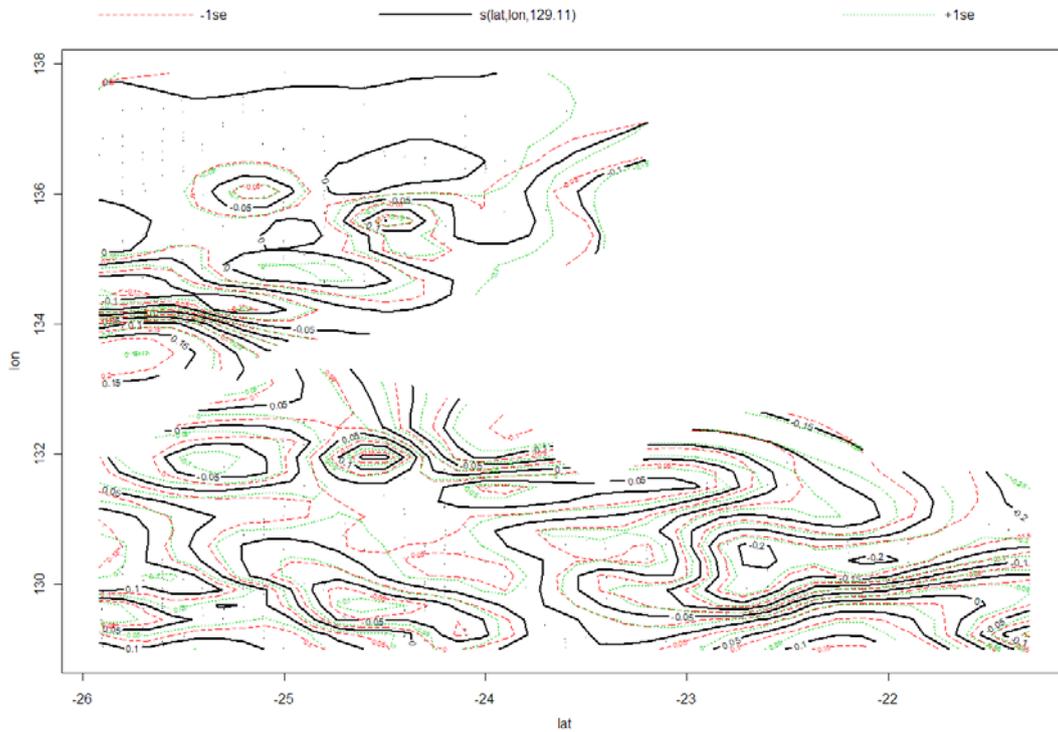
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Appendix

Outputs from the `mgcv` package for model checking

a)



b)

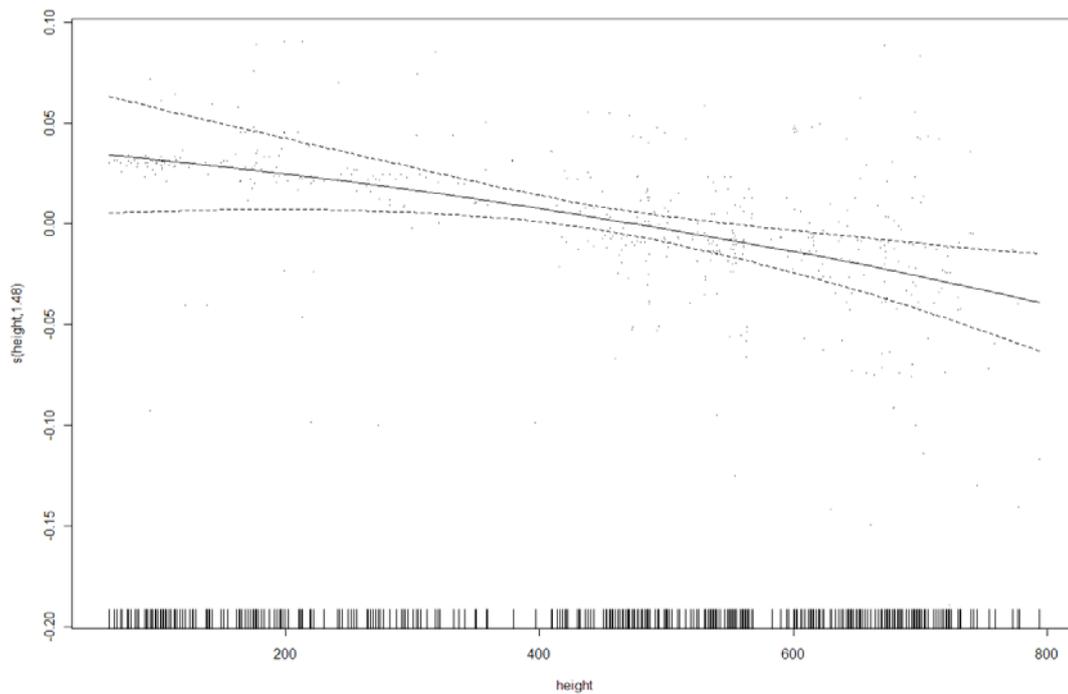


Figure 28: Fitted 'best' relationship between smoothed predictor variables a) latitude and longitude, and b) height above sea level (elevation) and the response variable camel density

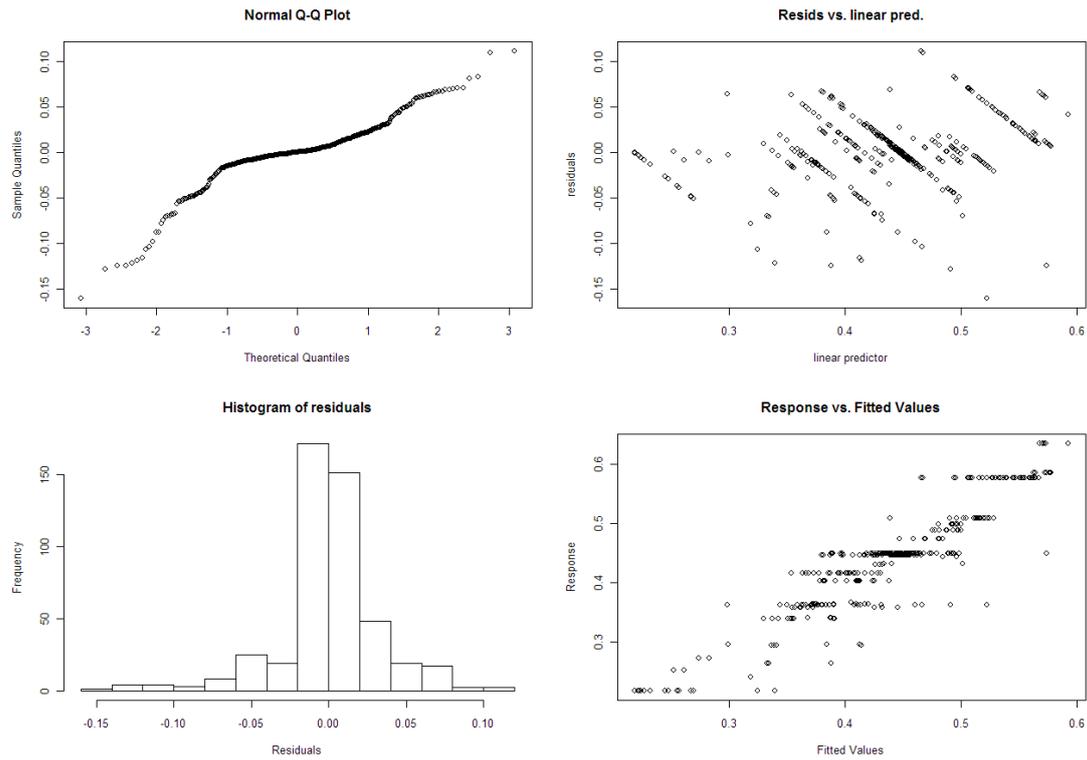


Figure 29: Basic plots for assessing whether the 'best' model of camel habitat preference meets underlying assumptions and is a reasonable fit to the data

Note: The lower right plot of response versus fitted values indicates reasonably good agreement between model predictions and observed data.

Summary of the best model

The following text is a screen dump of the best model from the habitat preference model using the R statistical analysis program and the `mgcv` package. Although the results indicated that one covariate was not significant (Bare), excluding it from the analysis resulted in a significantly poorer fit to the data because of interactions with other vegetation variables. We used the criteria described by Wood (2006) to determine whether or not to drop terms from the model.

Family: gaussian

Link function: identity

Formula:

stand.forage.ratio^0.25 ~ s(lat, lon, bs = "tp", k = 200) +
s(height) +

Shrubland + Grassland + Chenopod + Samphire + Bare

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	0.388145	0.008479	45.775	< 2e-16	***
Shrubland	0.072176	0.010217	7.065	9.22e-12	***
Grassland	0.036646	0.009430	3.886	0.000123	***
Chenopod	0.148613	0.021305	6.975	1.61e-11	***
Samphire	0.098102	0.023200	4.228	3.03e-05	***
Bare	0.032609	0.034570	0.943	0.346216	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Ref.df	F	p-value	
s(lat,lon)	129.105	129.605	10.433	< 2e-16	***
s(height)	1.475	1.975	5.265	0.00579	**

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq.(adj) = 0.779 Deviance explained = 84.2%

GCV score = 0.0028998 Scale est. = 0.00146 n = 474

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