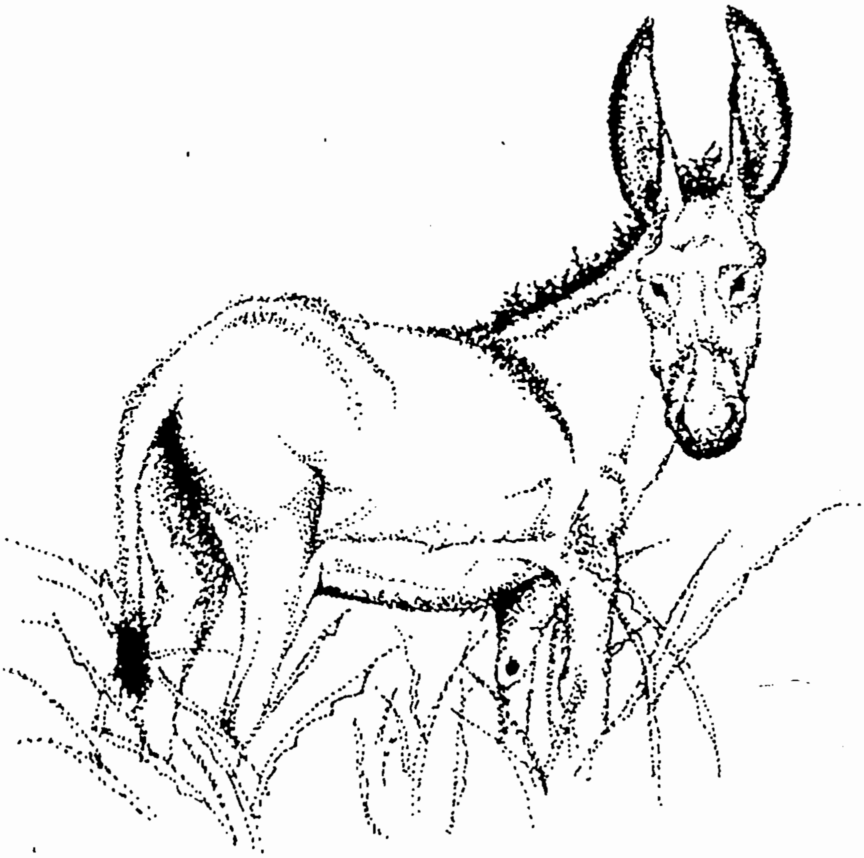
Feral Donkeys in Northern Australia: Population Dynamics and the Cost of Control.

By

David Choquenot (B.Sc.)



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SUMMARY

(1) Rate of increase was measured for feral donkey populations in parts of northern Australia as the average exponential rate of increase, r, in a population subjected to substantial reduction.

(2) The annual rate of increase was estimated to be r = 0.21. This estimate was compared with the exponential rate of increase in another recovering donkey population and found to be in close agreement.

(3) Ultimate and proximate factors regulating the abundance of feral donkey populations were examined by monitoring and sampling two populations; one at or close to equilibrium density, the other below equilibrium density and recovering from reduction.

(4) The size of the population at equilibrium density remained stable over the 12 months of monitoring while the size of the recovering population increased by 20 percent (r = 0.18/yr).

(5) Growth and body condition were significantly depressed in the population at equilibrium density suggesting that donkey populations are limited by the food resources available to them.

(6) Breeding occured over a discrete season, with births occurring between September and February.

(7) Fecundity was high, with more than 75 percent of mature females breeding in each year, and was independent of population density.

(8) Adult and juvenile mortality were density dependent, with mortality over the first six months of life the most important demographic factor influencing rate of increase in donkey populations, and hence population abundance.

(9) Implications of the estimated rate of population increase for the cost of long-term control of feral donkey populations were examined by constructing numerical models predicting the relative cost of ongoing control.

(10) These models were constructed using functions to describe density dependent variation in population productivity and the cost per donkey removed.

(11) The cost of removing donkeys at various population densities was estimated using predator-prey theory. The cost, measured in hours of helicopter time per removal, was found theoretically and empirically to take the form of an inverted functional response curve, with cost saturated at high donkey densities.

(12) The utility of models predicting the cost of continuing pest control is illustrated by comparing the relative costs of two potential strategies for feral donkey control.

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Section 1:

BACKGROUND TO THE STUDY

1.1 DYNAMICS AND MANAGEMENT OF ANIMAL POPULATIONS:

Biologists have been interested in growth and regulation of animal populations since an essay on the subject by Malthus (1798). Much of this interest has focused upon the dynamics of two types of animal; those that we exploit and those that we consider pests. Caughley (1976, 1977) suggests the reasons for this relate to the need to understand mechanisms influencing animal abundance so that animal populations might be managed to best conform to man's requirements. The management of animal populations is an exercise in applied population dynamics, hence some knowledge of these dynamics is an essential requirement for efficient population management. Caughley (1976) lists three discrete types of wildlife management, all of which require an understanding of dynamics of managed populations:

1. The manipulation of populations of rare species to increase abundance.

2. The manipulation of populations of exploited species to optimise offtake.

1.2 FERAL DONKEYS IN NORTHERN AUSTRALIA:

The donkey is an equid native to arid north-eastern Africa, that today enjoys an almost global domestic distribution (Lever 1985). Although feral populations are recognized from many areas within this distribution (Lever 1985), research on donkeys as an introduced species is restricted to North America (see Seegmiller & Ohmart 1981 for a review), the Galapagos Islands (Fowler de Neira & Johnson 1985) and northern Australia (McCool _et_ _al._ 1981a; current study).

Donkeys were first introduced into northern Australia for use in haulage teams during the mid 1800's and early 1900's (Letts _et_ _al._ 1979). Use of donkeys was particularly widespread in the Victoria River area of the Northern Territory and in the Kimberley pastoral district of Western Australia, where Kimberley Horse Disease or Walkabout Sickness, (an endemic toxic plant _Crotalaria_ _crispata_), restricted use of horses but did not effect donkeys (McCool _et_ _al._ 1981b). Following introduction of motorized transport to the area in the early 1900's, domesticated donkeys were liberated and large feral populations built up in parts of northern Australia (Lever 1985; McKnight 1976).

A report to the Northern Territory government (Letts *et al.* 1979) suggested that significant pasture degradation in the Victoria River District (VRD) and adjacent areas of Western Australia was caused by large numbers of feral donkeys (see also Wheeler 1987). The VRD is generally considered to be the area drained by the Victoria River which enters the sea on the north-west coast of Australia (Figure 1.1). The report recommended that the abundance of feral donkeys in the VRD be determined, and that if considered necessary, donkey densities be reduced (Letts *et al.* 1979). To meet these objectives the population of feral donkeys in the VRD was surveyed from the air in 1981 (Graham *et al.* 1982), extensively shot out between 1981 and 1984, and re-surveyed to assess the success of the control program at the conclusion of shooting in 1984.

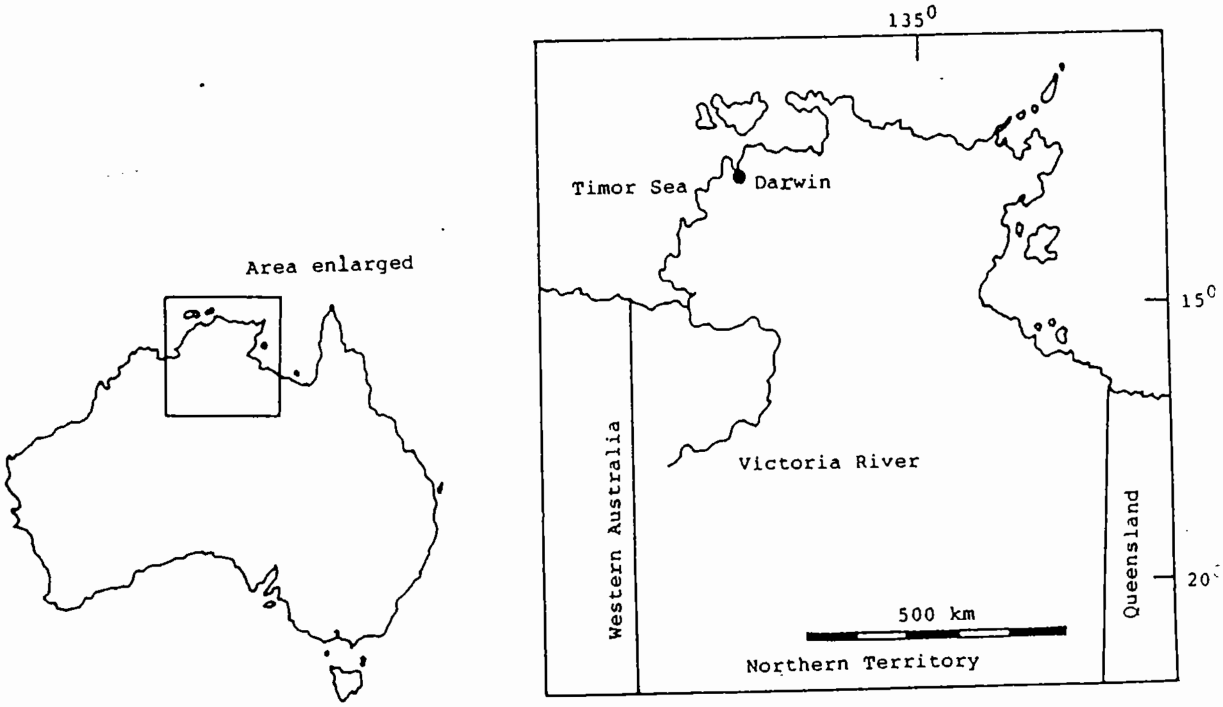

Figure 1.1 The general region of the study.

1.3 THE CURRENT STUDY:

The results of the 1981-84 VRD control program are examined in Section 2. Comparison of the pre- and post-shooting survey results examined in view of known rates of culling during the years of control demonstrated that feral donkey populations exhibited marked compensatory increases in abundance in response to reductions in population density.

The current study was initiated to fulfill the following aims:

1. To quantitatively determine the response of feral donkey populations to control by measuring the rate of increase (recovery) in another heavily-culled donkey population (Section 2).

2. To identify demographic parameters most influenced by population density, and hence most important in regulation of feral donkey populations through changes in the rate of population increase (Section 3).

3. To construct numerical models of the costs involved in control of donkey populations. These models are used to explore the implications that the rate of increase in culled

donkey populations have for efforts to establish control (Section 4).

1.4 THE REGION:

Study areas used were located in the VRD (Figure 1.2). The region contains habitat types varying from good pastoral range covered by three-awn (Aristida sp.) or spinifex (Triodia sp.) dominated plains to rugged hilly country unsuitable for stock (Perry 1970). Donkeys are found predominantly in the more rugged areas, particularly in locations containing broad, flat-topped mesa dissected by steep-sided wide valleys. This type of topography is characteristic of all study areas used in this project (Plates 1.1 and 1.2). Valleys dividing mesas typically contain tropical tallgrass savannah plains with an open eucalypt tree cover (Mott & Tothill 1984).

Climatic data from Timber Creek, a township central to all study areas, are summarised in Figure 1.3. Rainfall is abundant but highly seasonal, with all significant falls associated with the annual monsoonal wet season between November and March. The rest of the year is usually dry, with no substantial rainfall in most years. Daily maximum temperatures peak in the high 30's during the three months at the begining of the wet season, while minimum temperatures occur through the middle of the dry season.

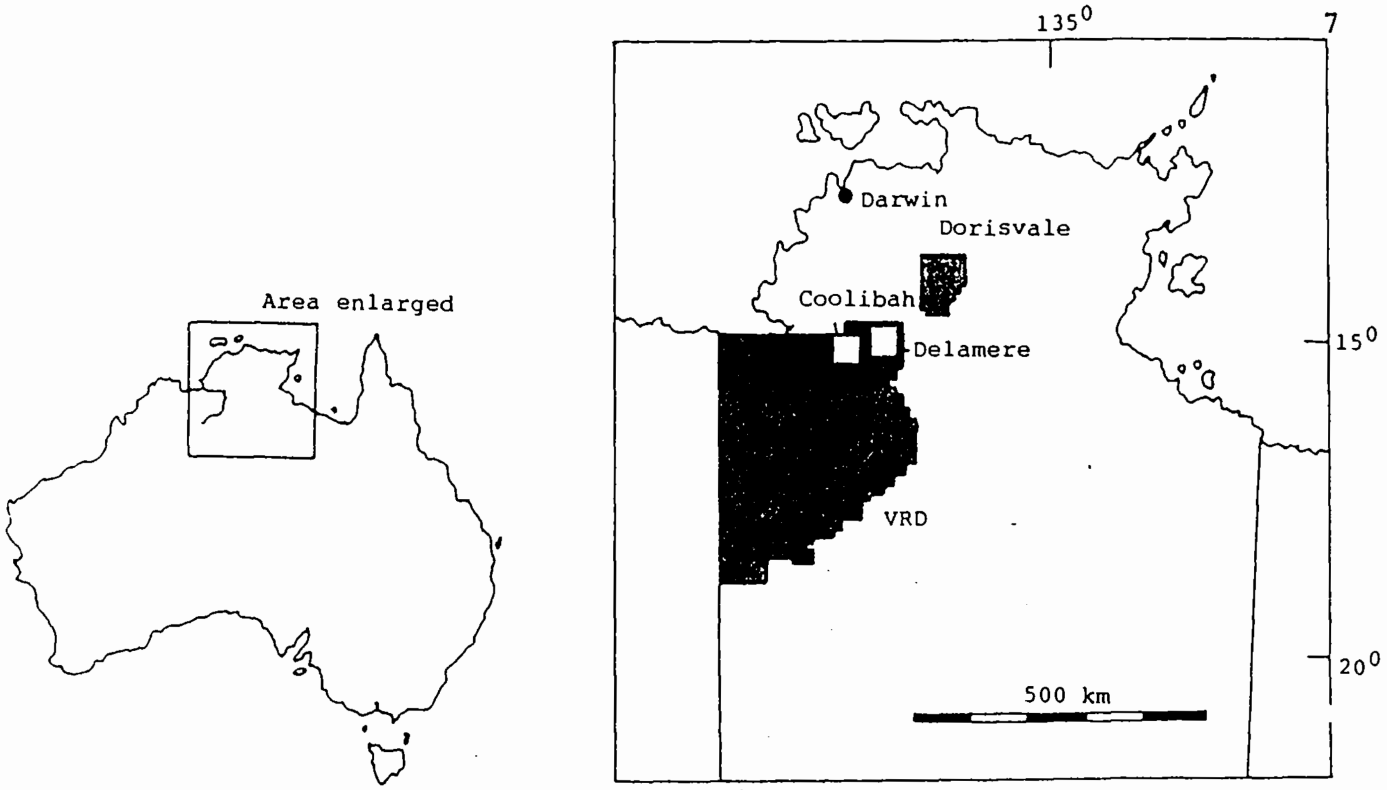

Figure 1.2 Study areas used during the project.

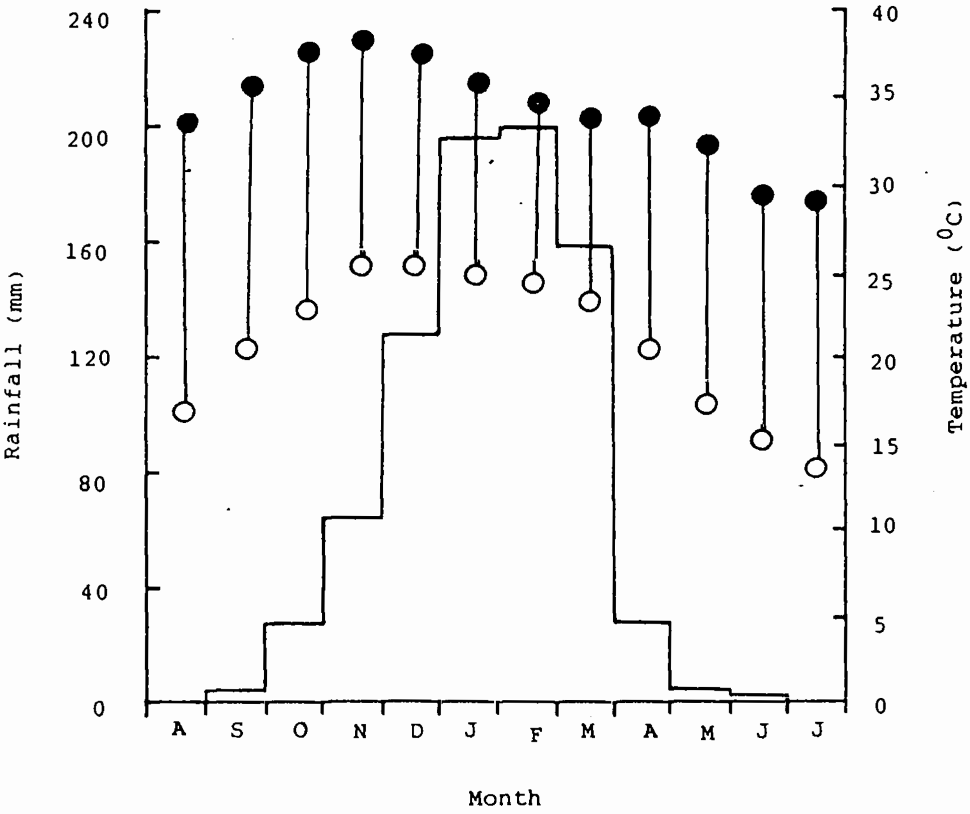

Figure 1.3 Summary of climatic data from Timber Creek collected between 1921 and 1987. The histogram gives average monthly rainfall (mm) and the bars associate average monthly maximum (●) and minimum (O) temperatures (°C).

Plate 1.1 A view looking north over the Coolibah study site. The topography is typical of that found throughout the Victoria River region. The Victoria River is in the foreground.

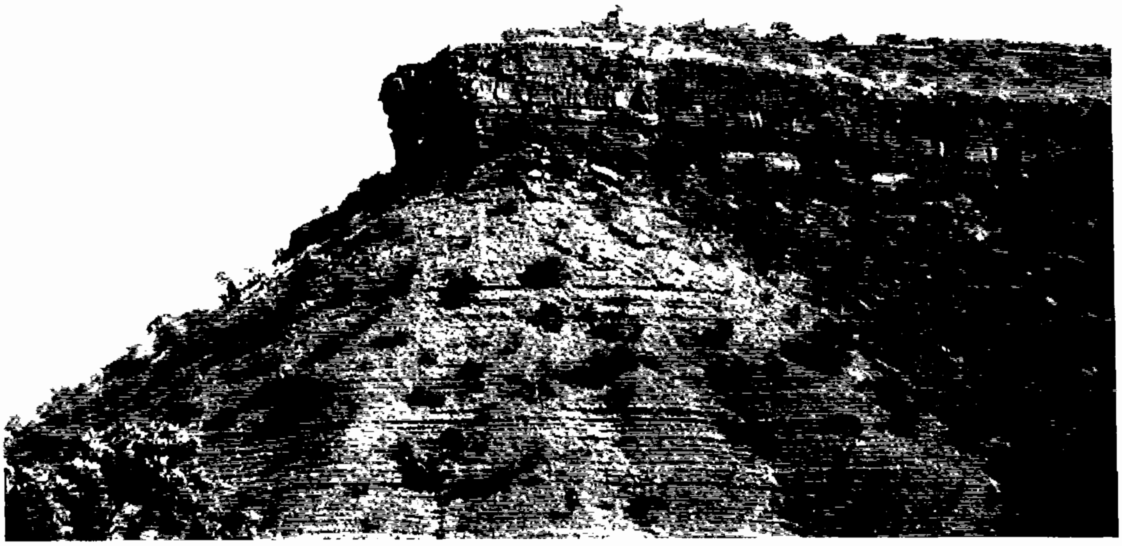

Plate 1.2 A view of the edge of one of the flat-topped mesas that characterise the Victoria River region. These high, rugged formations form extensive plateaux divided by broad grassy plains.

Section 2:

RATE OF POPULATION INCREASE

2.1 INTRODUCTION:

A population of animals reduced below equilibrium density generates a positive rate of increase (Andrewartha & Birch 1954; Lack 1954, 1966). Rate of increase provides important insights to the reaction of a population to its environment at any particular point in time. The intrinsic exponential rate of increase, r_{max}, measures a population's maximum capacity for increase in a given environment (Birch 1960; Caughley & Birch 1971). In food limited populations at densities below that at which food shortage imposes restriction on the rate of population increase, the observed exponential rate of increase, r_{obs}, coincides with r_{max} (Birch 1960; Caughley & Birch 1971; Caughley 1976, 1977 p.54; Caughley & Krebs 1983).

When control of a population is contemplated, the population's rate of increase determines how many animals must be removed from the population to restrain it at the desired level of abundance (Caughley 1976). Some knowledge of a population's potential rate of increase is required if the culling rate necessary to maintain control of the population is to be predicted (Caughley 1977 p.202)

This Section examines results of the 1981-84 VRD feral donkey control program. The rate at which the VRD population recovered following culling was measured directly as the average annual exponential rate of population increase (r), over the period of shooting. A second control operation (1985 Dorisvale program) involving the controlled reduction of an unshot population of donkeys and a subsequent series of surveys to monitor the rate of population recovery, is used to derive a second estimate of r for feral donkeys. This second estimate provides a comparison with r calculated from the VRD control program.

2.2 METHODS:

Study areas

The location of the two study areas is shown in Figure 2.1. The region in which the two study areas are located is described in detail in Section 1. The region is mainly occupied by leasehold cattle stations. Feral and domestic herds of both cattle and horses occur throughout the region (Graham _et_ _al._ 1982).

1981-84 VRD control program

The VRD control program consisted of a pre-shooting aerial survey of the areas donkey population in 1981 (Graham _et_ _al._ 1982), a shooting program in each year between 1981 and 1984, and a post shooting aerial survey in 1984. An area

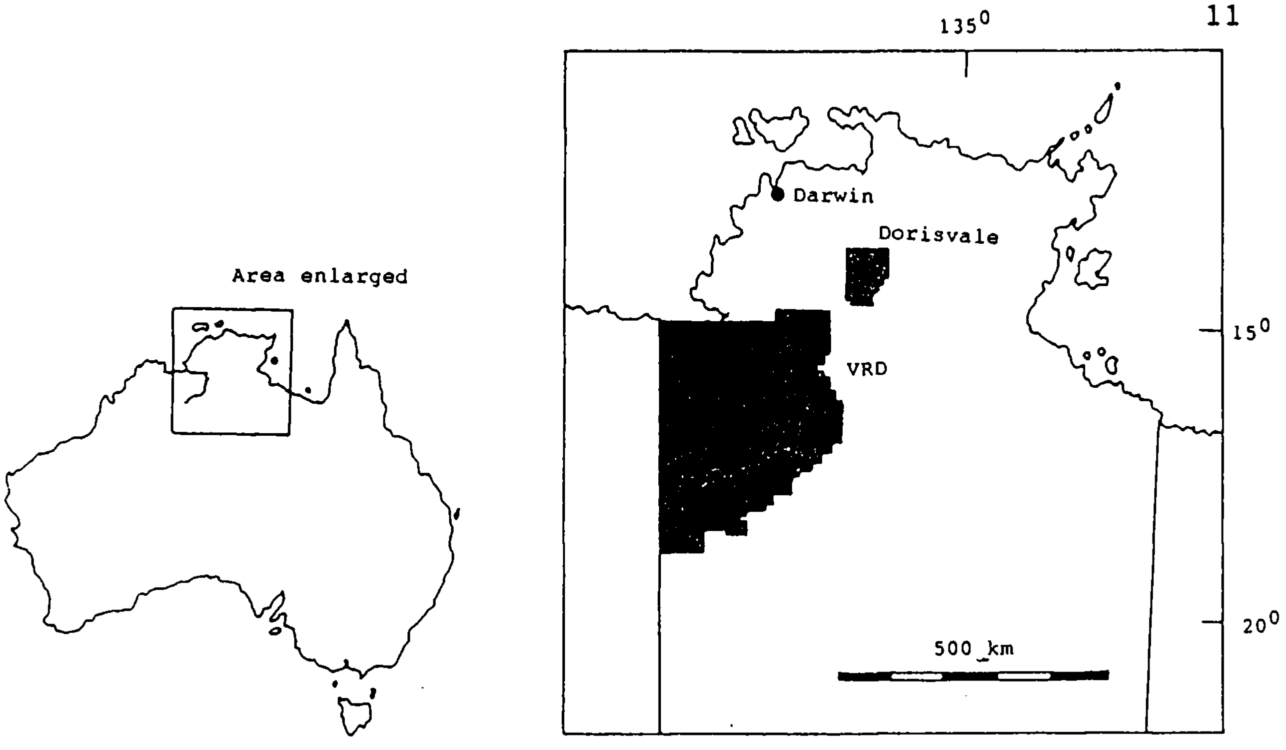

Figure 2.1 Location of the two study areas.

of 114,400 km^2 adjacent to the Western Australian border was covered during the control operation. The operation was the first attempt to control feral donkeys in part of their Northern Territory range (McCool et al. 1981b).

Pre-shooting and post-shooting aerial surveys were carried out from a Cessna 182 aircraft. Parallel east-west transects were laid across the area at 10 km intervals, and the aircraft navigated along these transects at a constant height of 76 m (250 ft) and a speed of 100 knts (130 km per hr). Two observers counted donkeys occuring in 250 m wide strips on either side of the aircraft, similar to the method for counting kangaroos (Macropus sp.) described by Caughley & Grigg (1981). Surveyed strips were demarked by the outside edge of the aircrafts wheels and fibre-glass rods attached to the wing supports. The number of individual donkeys were recorded in groups as they were seen by observers. Bayliss (1985a) estimated the sighting fraction for donkey groups counted from the air in open woodland habitat in northern Australia. Using a multiplicative correction factor of 2.3 to account for visibility bias associated with counts of donkey groups, the number of groups in each transect was estimated. These transect totals were multiplied by the mean size of donkey groups observed during each survey to estimate the number of individual donkeys in each transect. The ratio method (Jolly 1969; Caughley & Grigg 1981) was used to derive an estimate of the donkey population in the survey area.

All feral donkey control was carried out by shooting from helicopters during the dry season (April-September). Helicopter shooting is the most humane and efficient method of donkey destruction given the rugged topography of the region. The control program began in 1981 and concluded in 1984. The number of donkeys killed in each year of the operation and the general region in which kills were made were recorded.

1985 Dorisvale program

The 1985 Dorisvale program was designed to monitor the rate at which a donkey population recovered following a significant reduction. An area of 5,128 km^2 to the north of the VRD control area was surveyed from the air in October 1985 immediately after a donkey control operation was carried out. The area had contained a high density, unshot population of donkeys prior to control, which reduced the donkey population by approximately 80 percent. Two follow-up surveys were then performed in the area during July in 1986 and 1987.

Aerial surveys of the Dorisvale study area were carried out in the same way as those in the VRD program, except that aircraft height was 61 m (200 ft) and strips 200 m wide were surveyed on either side of the aircraft. Transects were also placed 5 km apart as opposed to 10 km during the VRD operation. No attempt has been made to correct the Dorisvale counts for visibility bias. Rather, raw counts (ie: counts uncorrected for visibility bias) have been used as simple indices to the size of the areas donkey population. Bayliss (1985a) demonstrated that population density had no detectable effect on the visibility bias associated with aerial counts of feral donkeys.

2.3 RESULTS:

Rate of population increase

1981-84 VRD control program:

Mean sizes of donkey groups for the 1981 and 1984 aerial surveys were 4.51 and 4.22 respectively. Table 2.1 gives total population and population density estimates for each survey of the control area. The difference between mean population estimates indicates a nett population reduction of 46 percent was achieved by the VRD operation.

Table 2.1 Population size, density (donkeys/km^2) estimates and their associated standard errors (SE) and standard error percentage (SE%) for the VRD feral donkey population, ascertained from aerial surveys in 1981 and 1984.

Year	Population size	SE	Density (Donkeys/km^2)	SE	SE%
1981	97,953	19,982	0.86	0.18	20
1984	52,760	11,158	0.46	0.10	21

Table 2.2 summarises the number of donkeys killed during each year of the control program. A total of 83,025 donkeys were removed from the VRD population during the four years of the control. This is equivalent to a reduction of nearly 85 percent of the mean pre-shooting population estimate.

Table 2.2 Annual and cumulative kill totals for the 1981-1984 VRD control operation

Year	Annual donkey kill	Cumulative donkey kill
1981	14,667	14,667
1982	30,214	44,881
1983	24,576	69,457
1984	13,568	83,025

Because the 1984 aerial survey immediately followed shooting for that year, only three annual responses to population reduction (1981, 1982 and 1983), are assessed here. If the population responses to reductions in population size operate as simple additive increases in population density, the numerical increase in the VRD donkey population over the three years of control can be estimated by:

$$(N_1 - K) + I = N_2 \quad (1)$$

where N_1 is the average population estimate for 1981, K is the total number of kills between 1981 and 1983, N_2 is the size of the population following the reduction imposed between 1981 and 1983, and I is the numerical population response to the reduction imposed. K was calculated by summing kills recorded between 1981 and 1983, N_2 was calculated as the number of kills recorded for 1984 added to the mean 1984 population estimate.

Equation (1) estimates a numerical increase in population size of I = 37,832 by:

$$(97,953 - 69,457) + 37,832 = 66,328$$

The numerical increase in the population over the control period is divided by 3 (the number of annual population responses to control), to give an average annual numerical increase (i) for the population of 12,611. i can be used to calculate the average annual exponential rate of population increase for the control area from the difference between the size of the population after shooting but before any compensatory population response (N_o), and the size of the population after compensatory response to the imposed reduction but before any subsequent shooting takes place (N_t).

N_o and N_t are approximated by:

$$N_o = nl + kl - i \qquad (2)$$

and

$$N_t = nl + kl \qquad (3)$$

respectively, where nl is the mean population estimate for 1984 and kl is the number of kills for 1984. N_o and N_t were calculated as:

$$N_o = 52{,}760 + 13{,}568 - 12{,}611 = 53{,}717$$

$$N_t = 52{,}760 + 13{,}568 = 66{,}328$$

The average annual exponential rate of population increase is then calculated by:

$$r_{obs} = \text{Log}_e \ (N_t/N_o) \qquad (4)$$

to give a value for r_{obs} of:

$$r_{obs} = \text{Log}_e \ (66{,}328/53{,}717) = 0.21$$

r_{obs} for the VRD donkey population corresponds to a finite rate of increase of 1.23 (23%) per annum, and a doubling time of 4 to 5 years.

1985 Dorisvale program:

Figure 2.2 relates logged abundance indices (Ln(n)), of the Dorisvale study areas donkey population to time in months (t), taking the first aerial count (October 1985) as t = 0. The exponential rate of increase, r, was 0.40 between 0 and 8 months (October 1985 to July 1986), and 0.22 between 8 and 20 months (July 1986 to July 1987). The average monthly change in the logged abundance index over the 20 months covered by the three surveys is shown as the dashed line in Figure 2.2, and is described by:

$$Ln(n) = 4.20 + 0.03\ (Months)$$

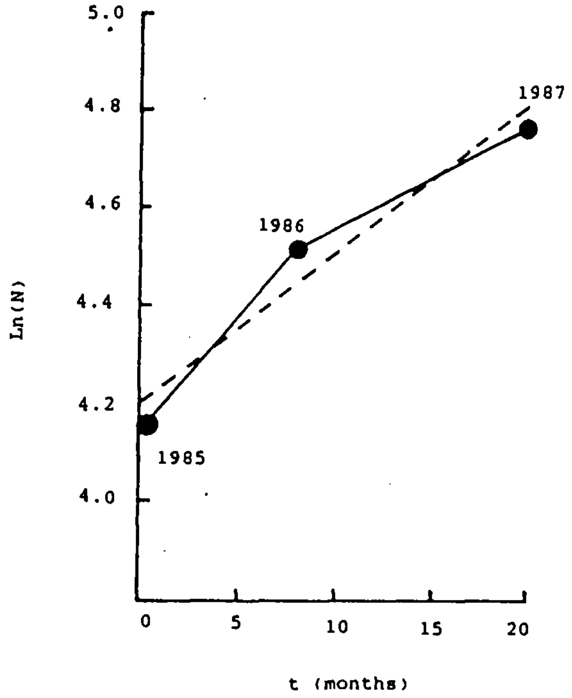

Figure 2.2 Logged abundance indices (Ln(n)) of the Dorisvale feral donkey population over time (t) in months. The dashed line is the least squares line of best fit indicating average monthly change in population abundance over the 20 months of monitoring (r^2 = 0.92).

The average monthly exponential rate of increase (0.03 ± 0.01) is equivalent to an average annual rate of increase of r_{obs} = 0.36 ± 0.12. The observed increase in population size over time is non-significant (F = 12.00, df = 1,1 NS) despite a very high correlation between the two variables (r = 0.96), probably because the data set is small (n = 3). It is proposed that some increase in the size of the population following reduction is a reasonable expectation (Caughley 1976). Hence, despite the non-significance of the observed increase in the Dorisvale population, it is accepted as real for further analysis and discussion.

2.4 DISCUSSION:

Observed rate of population increase

Average annual r_{obs} for the Dorisvale population (0.36) was not significantly higher than that for the VRD population (0.21) (T = 1.33, df = 1, NS). However, the rate of increase in the Dorisvale population appeared to slow considerably over time, with r_{obs} for the final 12 months (0.22) very similar to the average rate measured in the VRD population. There are several reasons to suspect that r_{obs} measured in the first 8 months of recovery ir the Dorisvale population may be artificially high, and hence not appropriate for extrapolation as a measure of the average rate of increase for the population.

Firstly, if the initial survey (t = 0) of the Dorisvale donkey population provided an inaccurately low index of abundance, estimates of the rate of increase in the population would be correspondingly high. The initial survey of the population was carried out immediately following a massive (80%) reduction of the area's donkey population. It is plausible that a percentage of the surviving donkeys had temporarily dispersed out of the area in response to the disturbance of shooting, or had congregated in denser stands of vegetation making them difficult to see from the air. Either instance would depress donkey counts, returning an artificially low index of the area's population abundance. If over the subsequent 8 months these donkeys moved back into the area or emerged from hiding, the second survey (t = 8) would have returned an accurate index of abundance leading to an inflated estimate of the population increase over the intervening 8 months.

Alternatively, a biased estimate of the population increase over the first 8 months of recovery may have occured because the initial survey (t = 0) took place in October, while the two subsequent surveys (t = 8 and t = 20) were both carried out in July. Donkeys in northern Australia have a discrete breeding season coinciding with the start of the monsoonal wet season (McCool _et_ _al._ 1981a; Section 3). The eight month period monitored by the first two surveys would have included most of this birth pulse, but only half of the subsequent dry season. If, as is likely, mortality in north Australian donkey populations occurs mostly during the dry season (see Section 3), the initial eight months of population monitoring would not have encompassed the full effects that annual mortality would have on the size of the population. Thus rate of population increase estimated over this period is likely to be inaccurately high. In contrast, the second and third surveys sampled a full twelve months of population growth and hence provide a more accurate estimate of the rate of increase for the population of donkeys in the area.

Taking these points into consideration, it seems likely that r_{obs} measured over the final twelve months of monitoring in the Dorisvale area provides a more accurate estimate of the donkey populations exponential rate of increase than does r_{obs} averaged over the entire twenty months of monitoring. Thus, the exponential rate of increase estimated from the VRD operation ($r = 0.20$) appears to be a good first approximation of the rate of increase in feral donkey populations in northern Australia.

The rate of increase in both the VRD and Dorisvale donkey populations was measured at densities around or below 50 percent of their initial abundance. At these densities, food should not represent a limiting factor to the rate of population growth (Caughley 1976; Fowler et al. 1980; Peek 1980; Caughley & Krebs 1983). Hence r_{obs} measured at these population densities should be coincident with the intrinsic rate of increase (r_m) for donkeys in northern Australia (Caughley 1976).

Comparison with other studies

Annual finite rates of increase for feral donkey populations in North America are reported to range from 1.2 to 29 percent (Morgart 1978; White 1980). Annual rate of increase in two North American feral horse (Equus caballus) herds was found to be 20 percent (Eberhardt et al. 1982; Eberhardt 1987). Such high rates of increase for feral equids have been questioned by Conley (1979) and Perryman & Muchlinski (1987), who argue that unrealistically high levels of fecundity would have to be realised by feral equid populations in order to generate rates of increase approaching 20 percent. In the study by Perryman & Muchlinski (1987), life-tables for feral donkeys were calculated from standing age distributions of a culled population in California. These life-tables were then used to construct Leslie matrix models (Leslie 1945, 1948), into which various age specific fecundity schedules were incorporated in order to examine how fecundity effected rates of population increase. Perryman & Muchlinski (1987) concluded that unrealistically high rates of fecundity (100% pregnancy rates) would have to be envisioned for a donkey population to generate a finite rate of increase approaching 20 percent per annum ($r = 0.18$). However, in constructing the life-tables upon which their matrix models are based, Perryman & Muchlinski (1987) have assumed that the standing age distribution of the donkey population is coincident with the temporal age distribution of a cohort, which gives the proportion of a cohort surviving to each age. Caughley (1977 p.88) points out that this assumption is only met for a population when r = 0. Perryman & Muchlinski (1987) have no knowledge of the rate at which their population is increasing, but given that the removals from which their age structures are derived represent significant proportions of the resident population, it is unlikely that r will be close to zero. The effect of this invalid assumption on Perryman & Muchlinski's (1987) life-tables will be to return significantly inflated estimates of age specific mortality rates. In order to compensate for inflated estimates of mortality and produce annual rates of increase approaching 20 percent, unrealistically high fecundity rates have to be incorporated into their matrix models. The current study estimated the finite rate of increase for donkey populations in northern Australia at about 23 percent. If mortality rates in recovering feral donkey populations are lower than Perryman & Muchlinski's (1987) analyses suggest, fecundity rates that have to be incorporated into matrix models to derive rates of population increase approaching 23 percent are also substantially lower, and hence more likely to occur in wild populations. Fecundity rates reported for donkey populations in northern Australia by McCool et al. (1981a) and in Section 3 indicate that greater than 75 percent of mature females breed annually. Such high fecundity would seem to indicate that feral donkey populations can and do undergo population recovery at rates approaching 20 percent per annum.

Section 3:

POPULATION REGULATION:
THE EFFECT OF POPULATION DENSITY ON GROWTH, BODY CONDITION AND DEMOGRAPHY

3.1 INTRODUCTION:

The rate of change in the size of a population is a function of the rates of addition and removal of individuals to and frpm the population. In animal populations, individuals are added through birth or immigration, and removed through death or emigration. These four factors collectively represent the demographic rates that are the proximate regulators of animal population abundance. Aspects of a populations environment (extrinsic factors) or social organisation (intrinsic factors) that affect demographic rates will ultimately determine whether the size of the population increases, decreases or stabilises. Hence, such factors represent the ultimate regulators of population abundance, which operate through changes in demographic rates (Lack 1954, 1966; Caughley & Birch 1971; Pianka 1974; Caughley & Krebs 1983).

Several authors have postulated that demographic rates (and hence the prevailing abundance) of populations of large mammals are regulated by extrinsic factors (Caughley 1970, 1976; Sinclair 1975, 1977; McCullough 1979; Sinclair *et al.* 1985). The two extrinsic factors most commonly invoked as the ultimate regulators of abundance in large mammal populations are food supply (Caughley 1970, 1976; Laws et al. 1975; Sinclair 1975, 1977; Houston 1982; Skogland 1983, 1985; Sinclair et al. 1985, Fryxell 1987), predation (Bergerud 1980; Gasaway et al. 1983; Messier & Crete 1984, 1985) or both (Caughley 1976).

Hypotheses that relate population regulation to food resources can be generalised to propose that density dependent changes in demographic rates regulate population abundance through food shortage (Lack 1954, 1966; Caughley 1970, 1976; Sinclair 1975, 1977; McCullough 1979). Section 2 estimated the rate of population increase in feral donkey populations in northern Australia recovering after being reduced below equilibrium density. This section attempts to answer two questions related to feral donkey population increase and hence population regulation:

1. What factors regulate the size of feral donkey populations (ultimate regulators)?

2. What demographic characteristics influence the rate of increase in feral donkey populations (proximate regulators)?

The first question was examined by attempting to test whether food resources ultimately regulated feral donkey population abundance. The food hypothesis predicts that a population at equilibrium density will suffer food shortage, while a population below equilibrium density will not. Growth rate and body condition were examined in a donkey population at or close to equilibrium density, and a population reduced to a significantly lower density. It was predicted that if food resources limited the size of donkey populations, donkeys from the high density population should have slower growth and poorer body condition than those from the lower density population due to increased competition for food at high density (Dauphine 1976; Mitchell et al. 1976; Skogland 1983; Messier & Crete 1984).

To examine the second question, age specific rates of reproduction and mortality were examined in the two populations, to determine what changes in demography were most important in modifying the rate of increase in donkey populations. Caughley & Birch (1971) demonstrated that the rate of increase in a population is dependent upon the populations age structure, sex ratio and age-specific rates of fecundity and mortality. Hence the demographic features which vary most significantly with prevailing population density will represent the proximate regulators of population abundance (Skogland 1985).

3.2 METHODS:

Study areas

Each study area was 225 km^2 (15 X 15 km) and was located within the Victoria River region (Figure 3.1). A description of the general area is given in Section 1.

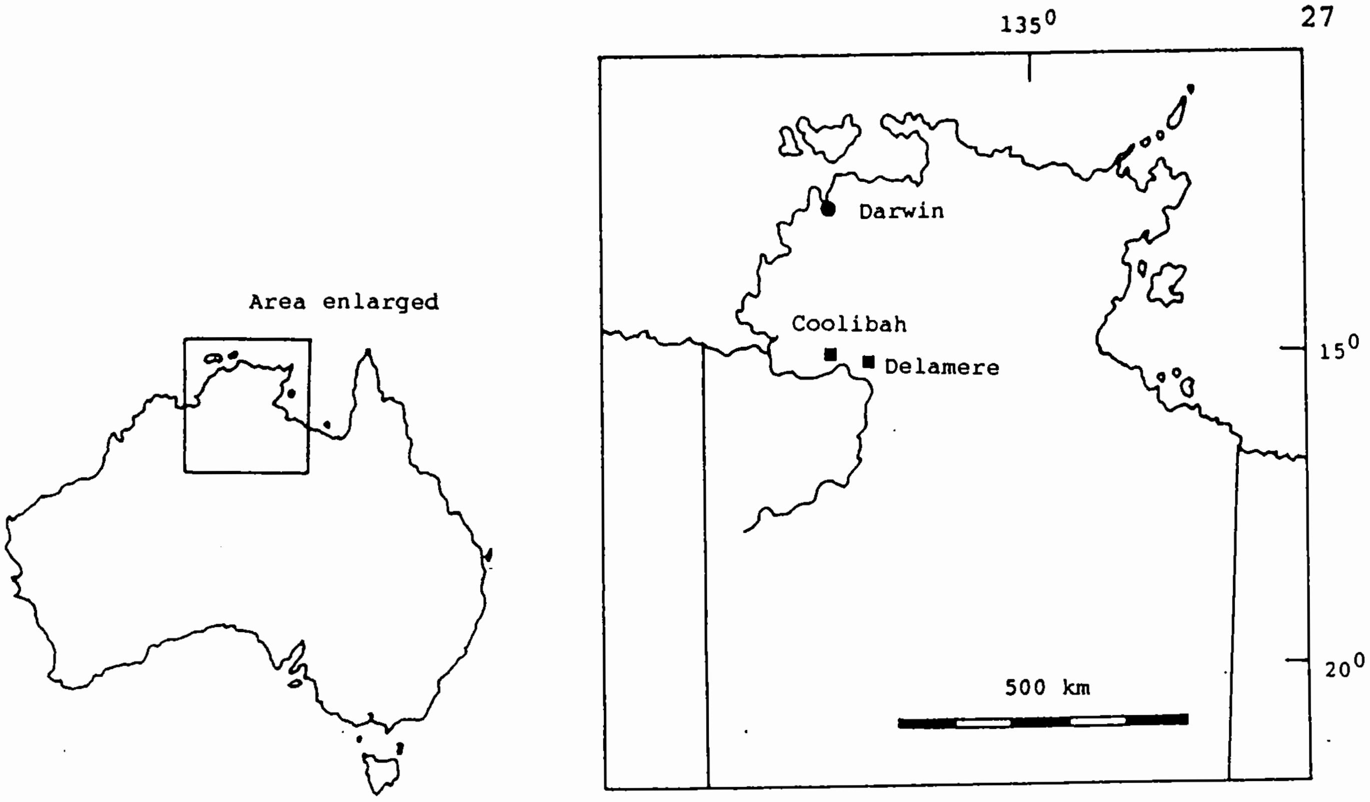

Figure 3.1 Location of study sites

Both areas contained high density (>10 donkeys per km^2), unculled populations of feral donkeys in 1981 (Graham et al. 1982).. In 1982 and 1983 one of these areas (Delamere) was subjected to an extensive donkey control program (see Section 2), which substantially reduced the density of donkeys (B. Walsh pers. comm.). No further donkey control work was performed in the Delamere area after 1983. No feral donkey control work has ever been carried out in the Coolibah study area.

Population monitoring

Donkey populations in the two areas were surveyed from helicopter in July of 1986 and 1987. Twenty parallel strip transects running east-west were used to sample the donkey population in each area. A single observer counted donkeys occuring in groups within a 150 m wide survey strip along each of the transects (sampling rate = 20%). Survey strips were demarked by a pole attached to the side of the helicopter. Helicopter height was 46 m (150 ft) and nominal airspeed was 50 km per hr, although airspeed varied somewhat with terrain. Donkey counts in each transect were converted to densities of donkeys counted per km^2. The density of donkey counts was used as an index of population density. Bayliss (1985a) demonstrated that aerial counts of donkeys are not effected by prevailing donkey density. The simple method (Caughley 1977 p.30) was used to estimate the average density of donkeys counted in each area for the 1986 and 1987 surveys.

Population sampling

150 donkeys were sampled from each population immediately after the first aerial survey was completed in 1986. Donkeys were sampled by shooting from helicopter. An attempt was made to shoot any donkey seen in order to randomise sampling as much as possible (during helicopter shooting each donkey seen has an equal chance of being shot). Autopsies were carried out on site. All donkeys sampled were examined for scarring consistent with attack by wild dogs or dingos (Canis familiaris), both of which occur in the region (McCool et al. 1981a).

Aging

Donkeys were aged in years using general equid tooth eruption and wear criteria (Davis 1966; Klingel & Klingel 1966; Woodward 1976; Ruffner & Carothers 1982). No attempt was made to age donkeys more precisely than given year classes. As sampling occured seven to eight months after the season of births (McCool _et_ _al._ 1981a; and see this Section later), donkeys considered to be less than one year old were assigned to a 0.5 age class, those one to two years old were assigned to a 1.5 year age class, those two to three years old were assigned to a 2.5 year age class, and so forth. Donkeys less than 2.5 years old could be confidently assigned to year classes on the basis of tooth eruption alone (Woodward 1976; Ruffner & Carothers 1982; Johnson _et_ _al._ 1987). However, aging older donkeys required additional assessment of tooth wear patterns. This introduced some degree of subjectivity in age determinations, and with it the potential for error. The accuracy of the visual age determinations was tested for donkeys two years and older by independently aging 140 donkeys by microscopic examination of cementum annuli in the primary permanent incisor (I_1) (Low & Cowan 1963; Reimers & Nordby 1968; Spinage 1976). Spinage (1976) found that cementum aging was an appropriate technique for use with mammals (particularly ungulates), in areas of sub-tropical Africa characterised by a uni-modal rainfall pattern similar to that occuring in northern

Australia. As such, it is expected that the cementum annuli counted in the primary incisors of donkeys examined in this study should correspond to sequential, annual tooth growth increments. Hence counts of cementum annuli should indicate the number of years following eruption of the primary incisor and therefore the age of the donkeys.

Growth and body condition

Head length (mm) was measured from between the ears to the most anterior margin of the nostrils using a flexible fibre-glass tape, and is used here as the primary measure of donkey size.

Body condition was assessed using the kidney-fat-index (KFI) (Riney 1955; Hanks 1981). The left kidney and its associated perirenal fat (cut through at the caudal pole of the kidney) were removed from each donkey. The weight (gms) of the kidney and associated fat was divided by the weight of the kidney alone and multiplied by 100 to derive the KFI.

Reproduction

Sexual maturity in males was assessed by microscopic examination of a smear taken from the epididymes. If sperm were present in the smear the donkey was considered mature.

Females were examined for lactation, pregnancy and ovarian activity. When pregnant, foetal crown-rump length (mm) and sex were recorded. Non-pregnant females were examined for ovarian activity. Females were considered to be mature (cycling) if mature follicles (>2cm diameter), corpora lutea or corpora haemorhagica were detected. The frequency of pregnant females in age specific samples was used to calculate age specific fecundity rates for each population. Fecundity was calculated as m_x, the number of female offspring produced per female per year at age x.

In the absence of data on donkey foetal development, approximate foetal ages were calculated using the relationship between foetal age in days and foetal crown rump length (mm) for horses reported by Fraser (1971). Foetal age and crown-rump length scales were adjusted to values appropriate for donkeys according to ratios given by McCool et al. (1981a). Donkeys have a gestation period of around 12 months (Walker 1975; McCool et al. 1981a, Perryman & Muchlinski 1987), and hence foetal age indicates the approximate date of both conception and birth. Median and mean birth/conception dates, along with associated standard deviations and standard errors were calculated from distributions of foetal ages according to Caughley (1977 p.73)

Mortality

Age specific mortality rate (q_x) was calculated for each population from smoothed age distributions (F_x), using

Caughley's (1977 p.92) method 6. F_x was calculated using a probit transformation (Caughley 1970, 1977 p.96) to smooth standing age distributions (f_x). The frequency of zero age classes were calculated from m_x schedules and the observed age distribution of each population. F_x is multiplied by e^{rx} (where r is the exponential rate of population increase) and then divided by F_0 to give a survival series (l_x schedule) for the population. Mortality (d_x) and its associated mortality rate (q_x) were calculated from the l_x series.

3.3 RESULTS:

Population monitoring

The average density of donkey counts for each area in 1986 and 1987 are shown in Figure 3.2. The low density population in 1986 had a density 45 percent of the high density population. The twenty sampled transects in each area were used to test for significant variation in the density of donkeys counted between years. A mixed-model analysis of variance was used to remove transect effects, before testing for differences over time (years). The decrease (-3%) in density of donkeys counted between 1986 and 1987 in the high density population was non-significant (Table 3.1a). There was a significant increase (+20%) in the density of donkey counts in the low density population over the same period (Table 3.1b).

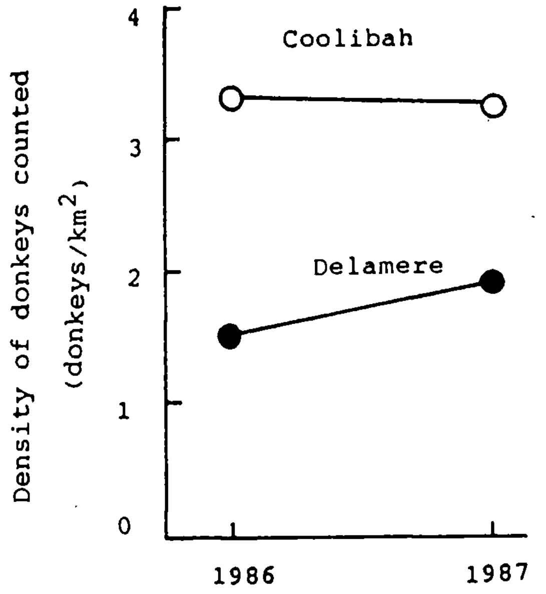

Figure 3.2 Average density of donkeys counted in the two study areas in 1986 and 1987.

Table 3.1 Mixed-model ANOVAs describing variation in the density of donkeys counted in (a) the high density population, and (b) the low density population, in 1986 and 1987 (Year). Transects have been entered into the analyses as a continuous variable to remove transect effects before testing between years in each area.

Source	df	SS	MS	F	p
(a) High density					
Transects	19	463.6	24.4	14.67	<0.001
Year	1	0.4	0.4	0.24	NS
Error	19	31.6	1.7		
Total	39	495.6			
(b) Low density					
Transects	19	194.4	10.2	15.10	<0.001
Year	1	5.6	5.6	8.30	<0.01
Error	19	12.0	0.7		
Total	39	212.0			

Aging

Assuming that ages calculated using cementum annuli are accurate, comparison between cementum ages of individuals and their visually appraised ages can be used to assess the accuracy of the visual aging technique. When visually assigned ages were regressed on cementum age, the intercept of the least-squares line of best fit was not significantly different to zero (t = -1.18, df = 138, NS). This indicates that the line describing the relationship between the two aging techniques passed through the origin of the x and y axes. When the regression was recalculated and forced through the origin, the slope of the line of best fit was not significantly different from one (t = 1.11, df = 139, NS) demonstrating that visually assessed ages were, on average, the same as those derived from counts of cementum annuli and hence accurate. To assess the precision of year class estimates for samples used in this study, ninety-five percent confidence intervals around visually aged samples between 2.5 and 10.5 years were calculated from the residual variation in visual age estimates assuming cementum ages are accurate (Table 3.2). The magnitude of the calculated confidence intervals never exceeded 1.0, indicating that if a sample the same size as that given for each age class in table 3.2 is placed in that year class, ninety-five percent of the assessed ages will be accurate to within one year. Sample sizes for age estimates older than 10.5 years were too small for realistic assessment of accuracy or precision. As such, donkeys aged 10.5 years and older have been combined into single age classes.

Table 3.2 Magnitude of 95 percent confidence intervals around visual age estimates between 2.5 and 10.5 years for feral donkeys. Confidence intervals are for samples of size n measured from residual variation assuming cementum ages are accurate.

Year class	Magnitude of 95% confidence interval	n
2.5	0.21	14
3.5	0.20	30
4.5	0.25	27
5.5	0.29	15
6.5	0.95	14
7.5	0.24	12
8.5	0.86	18
9.5	0.63	5
10.5	0.58	5

Growth

Growth in head-length (age specific head-length) was not sexually dimorphic. 282 head-lengths were measured overall; 142 from the high density Coolibah population, and 140 from the low density Delamere population. Analysis of variation in head length due to sex and age yielded no significant interaction (Table 3.3), hence male and female samples have been combined in further analyses of growth.

Table 3.3 ANOVA table assessing variation in head-length due to age and sex in feral donkeys. An unweighted means solution (Freund & Littell 1981) was used to account for the unbalanced design.

Source	df	SS	MS	F	p
Age	10	374928.6	37492.9	39.3	<0.001
Sex	1	37.7	37.7	0.1	NS
Age X Sex	10	7276.3	726.7	0.8	NS
Error	260	248242.2	954.8		
Total	281	632315.1			

Growth is dependent on population density. Figure 3.3 shows average head-length on age for high and low density populations. Growth continues until some age between 2.5 and 3.5 years, when maximum size is attained. Donkeys 3.5 years or older have been combined into a single $\geq$3.5 year age class. Table 3.4 gives the average age specific head-lengths for donkeys in each population. When variation in head-length due to age and population density is examined (Table 3.5), the significant interaction between population density and age demonstrates that growth in donkeys is dependent upon population density. Paired comparisons between mean head-lengths at high and low population densities for each age class (Table 3.6), indicate that growth differs between populations only over the first 2.5 years of life.

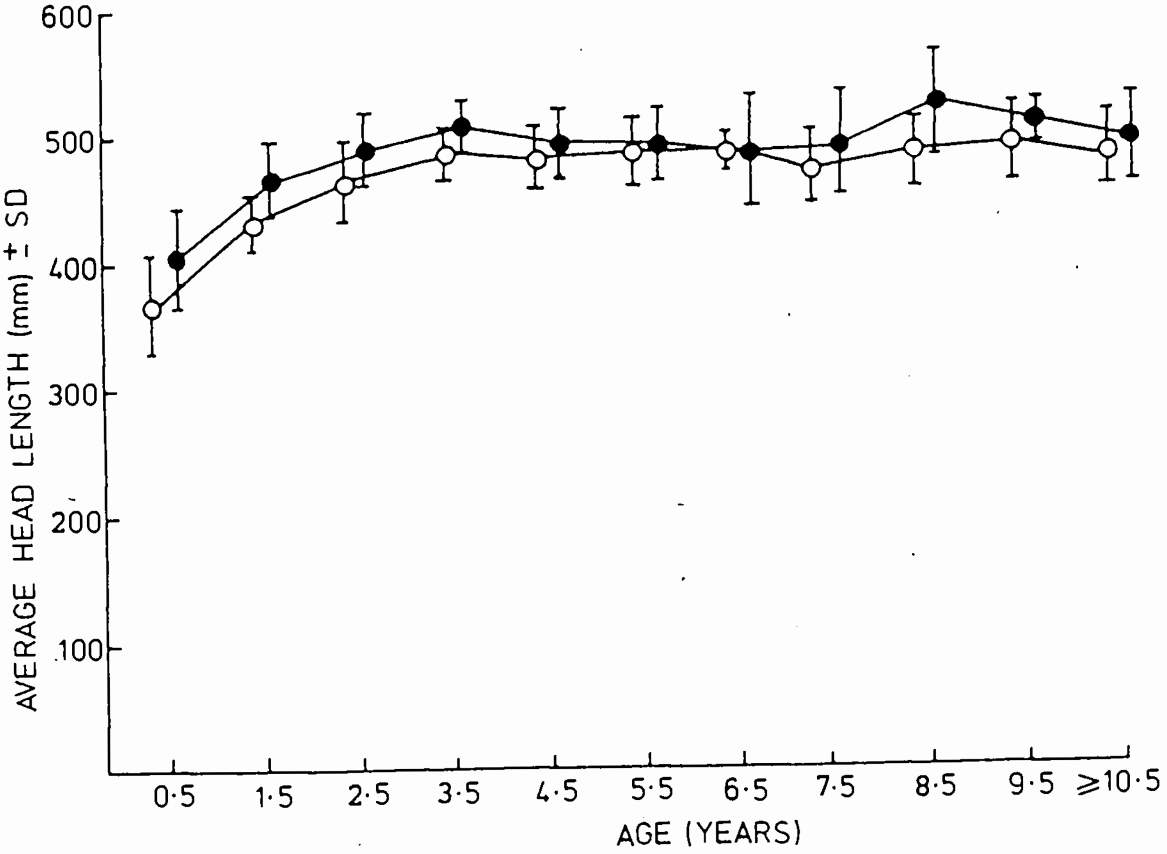

Figure 3.3 Growth of donkeys in high density (O) and low density (●) populations. Values are average head length ± one standard deviation.

Table 3.4 Average age specific head-lengths (mm) ± standard errors of donkeys from high (H) and low (L) density populations. Sample sizes are given in parentheses.

	0.5 yr.	1.5 yr.	2.5 yr.	≥3.5 yr.
H:	366 ± 9 (15)	446 ± 5 (30)	481 ± 7 (11)	484 ± 2 (88)
L:	398 ± 9 (18)	472 ± 6 (19)	482 ± 7 (24)	493 ± 3 (77)

Table 3.5 ANOVA table assessing variation in head-length for donkeys due to age and population density. An unweighted means solution (Freund & Littell 1981) was used to account for the unbalanced design.

Source	df	SS	MS	F	p
Age	3	391348.4	130449.5	160.4	<0.001
Density	1	32309.1	32309.1	39.7	<0.001
Age X Density	3	7521.7	2507.2	3.1	<0.05
Error	274	222872.1	813.4		
Total	281	632315.1			

Table 3.6 Paired comparisons of age specific average head-length between high and low density donkey populations.

Age class	t	df	p
0.5	3.15	51	<0.001
1.5	3.68	36	<0.001
2.5	2.40	29	<0.05
$\geq$3.5	1.78	15S	NS

Body condition

KFI were obtained from 59 males and 87 females in the high density population, and from 70 males and 65 females in the low density population. Figure 3.4 shows age specific average KFI for each sex from each population. Donkeys 10.5 years and older have been combined into single age classes.

Analysis of variation in KFI due to population density and sex demonstrated that KFI was both density dependent and

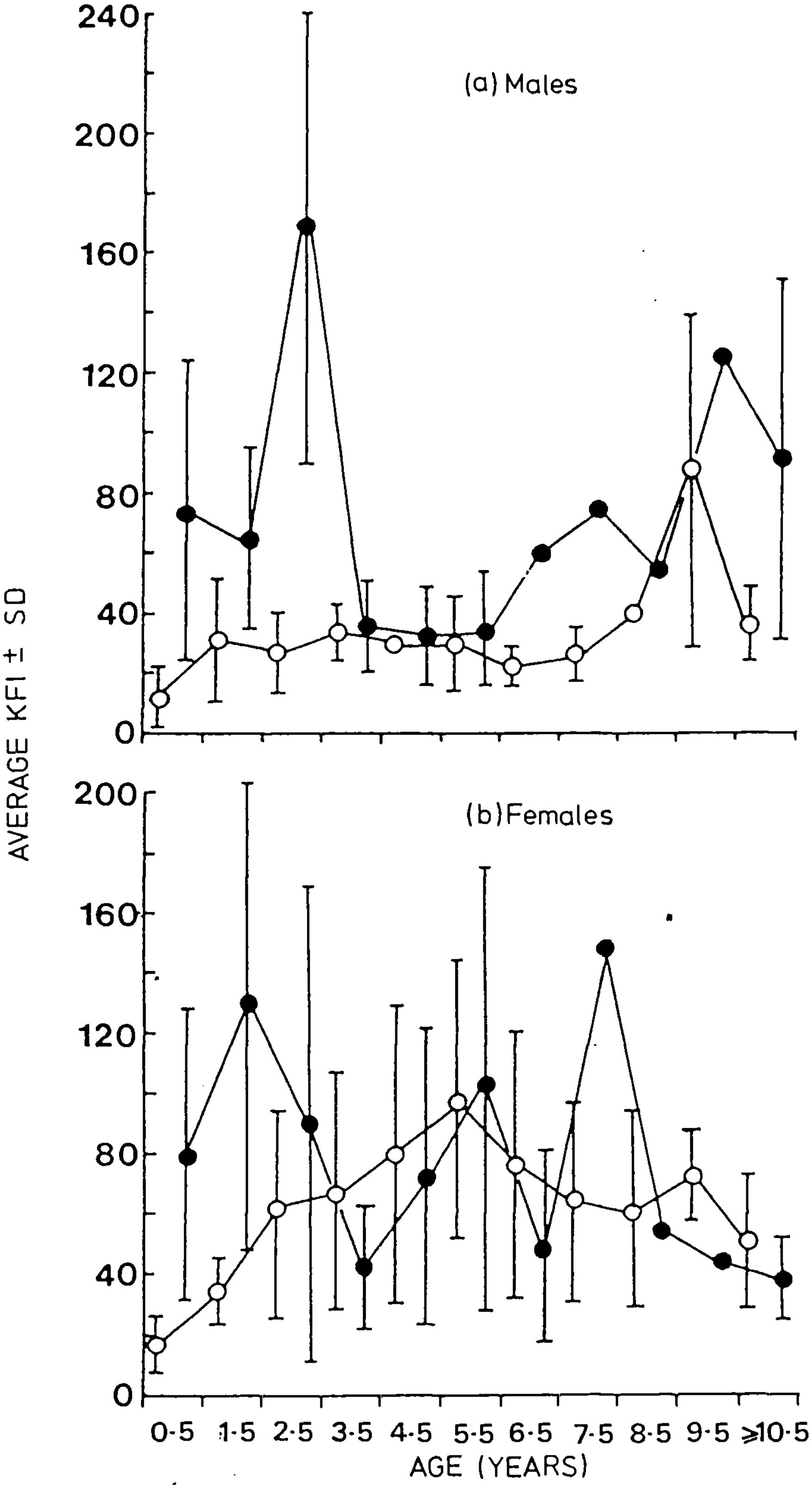

Figure 3.4 Average age specific KFI (± one standard deviation) at high (O) and low (●) population densities for (a) males and (b) females.

sexually dimorphic (Table 3.7). The lack of significant interaction between the two factors suggests that the observed sexual dimorphism in KFI was not density dependent. Further analyses of variation in KFI were therefore performed separately on the four subpopulations defined by sex and population density. When each sex/density subpopulation was considered separately, KFI varied significantly with age in the high density population only (Table 3.8). Examination of mean age specific KFI for the high density population (Figure 3.4) suggests that low KFI values in the youngest age classes (ie: <3.5 years) of both sexes were the probable cause of significant age related variation in KFI. To test this, donkeys 3.5 years or older were combined in a single age class and variation in KFI due to age was reassessed with age classes progressively excluded from the analyses, from youngest to oldest (Table 3.9). The results indicated that variation in KFI in donkeys from the high density population was not related to age in males from age classes older than 0.5 years, and in females from age classes older than 1.5 years. Figure 3.5 summarises these results more explicitly, indicating the mean KFI in each subpopulation which is significantly different from other subpopulations. Donkeys from the high density population have consistently lower KFI than do those from the low density population. Within populations females have consistently higher KFI than do males. At low population density KFI values are not age related, while at high population density the youngest donkeys of both sexes have significantly depressed KFI.

Table 3.7 ANOVA table assessing variation in KFI of donkeys due to population density and sex. An unweighted means solution (Freund & Littell 1981) was used to account for the unbalanced design.

Source	df	SS	MS	F	p
Density	1	58773.0	58773.0	19.2	<0.001
Sex	1	21897.1	21897.1	7.2	<0.01
Density X Sex	1	9358.4	9358.4	3.1	NS
Error	289	885116.0	3062.7		
Total	292	967782.9			

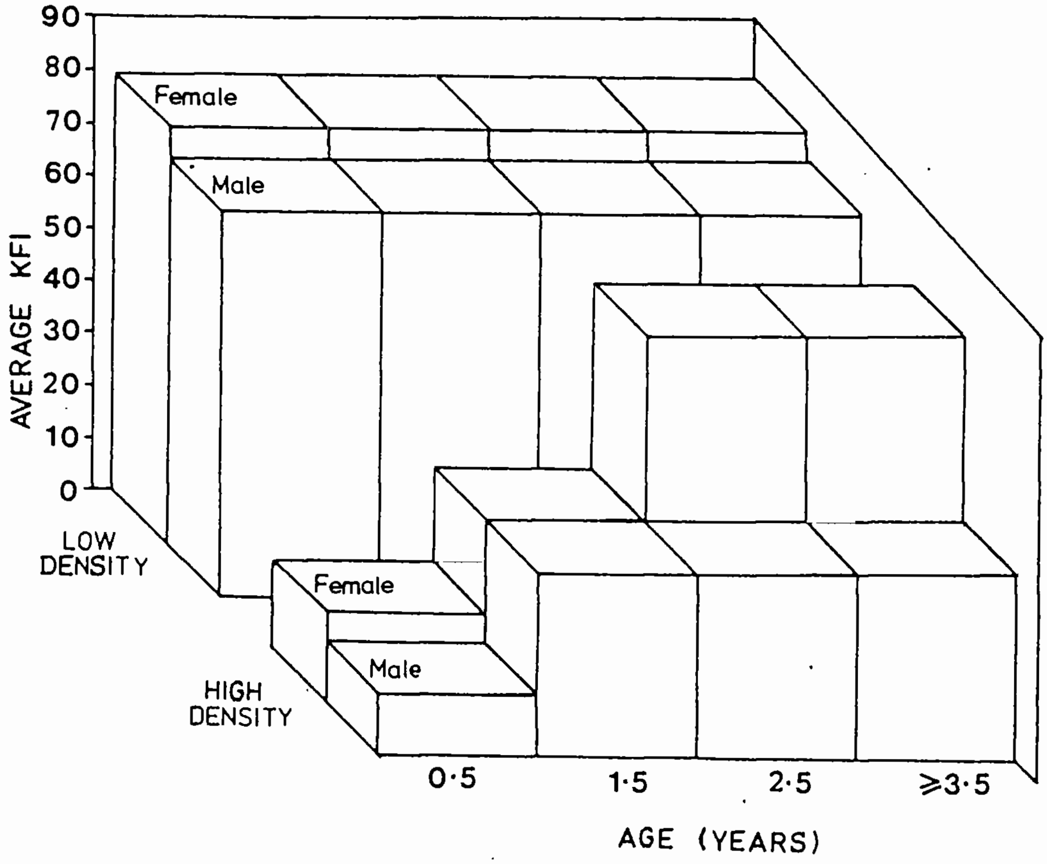

Figure 3.5 Summary of significant sex, density and age specific differences in KFI.

Table 3.8 Summary of ANOVA results for assessment of variation in KFI due to age in each density/sex subpopulation of donkeys. Unweighted means solution (Freund & Littell 1981) has been used in each analysis to account for the unbalanced design.

Density	Sex	df	F	p
High	Males	10,50	4.4	<0.001
High	Females	10,71	2.8	<0.01
Low	Males	10,62	1.8	NS
Low	Females	10,51	1.9	NS

Table 3.9 Summary of ANOVA results assessing variation in KFI due to age for male and female donkeys at high population density, with age classes sequentially excluded from youngest to oldest. An unweighted means solution (Freund & Littell 1981) has been used to account for the unbalanced design.

Sex	Age classes excluded	df	F	p
Males	None	3,57	2.9	<0.05
Males	0.5	2,49	0.6	NS
Females	None	3,78	7.1	<0.01
Females	0.5	2,71	3.2	<0.05
Females	0.5,1.5	1,65	0.5	NS

Reproduction

Male donkeys from the low density population appear, on average, to attain sexual maturity at earlier ages than males from the high density population. Males were assessed either as active (sperm present in epididymeal smear) or inactive (no sperm present). The percentage of active males in age specific samples from each population are shown in Figure 3.6.

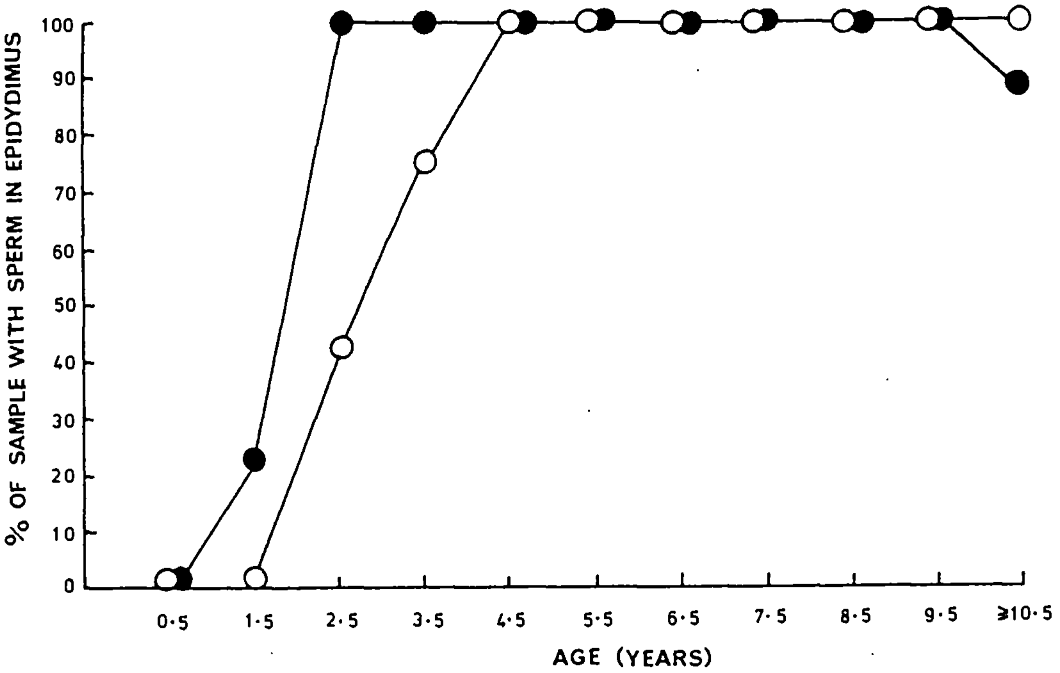

Figure 3.6 Percentage of males in each age-class with sperm present in epidydimeal smears at high (O) and low (●) population density.

To test for population differences in the proportion of mature males in each age class, observed age specific frequencies of mature males were tested against an expected equal distribution of mature males between the two populations (Table 3.10). The difference in the observed frequency of mature males in the two populations was only significant for the 2.5 year age class. One presumably sensescent male was found in the low density population.

This individual was aged visually at >20 years and had degenerated testes.

Table 3.10 Tests for age specific differences in the percentage of mature males at high and low population density. Observed percentages of mature males were compared with an expected even distribution of mature males between populations. Test statistics (dependent upon sample size) are *Chi-square with Yates correction or **Fisher's exact probability test.

Age	Test statistic	p
1.5	1.01*	NS
2.5	0.03**	<0.05
3.5	1.44**	NS
>10.5	1.00**	NS

104 pregnant females were sampled. The foetal sex ratio did not differ from 1:1 in either population (Table 3.11).

Table 3.11 Tests for departures from an expected 1:1 foetal sex ratio in high and low density donkey populations.

Population	n	df	X^2	p
High density	53	1	0.93	NS
Low density	32	1	1.13	NS
Both	85	1	1.99	NS

A curve was fitted to the relationship between foetal crown-rump length and foetal age to allow approximate foetal age to be predicted. The relationship was described by:

$$\text{Age (days)} = 41.37 \{\text{Ln foetal crown-rump length (mm)}\}$$

The relationship was highly significant ($F = 163.47$, df = 1,9, $p < 0.01$), and is shown in Figure 3.7.

Median, and mean birth/conception dates, along with associated standard deviations and standard errors are given Table 3.12. There was no significant difference between median birth/conception dates for each population ($U = 1041.5$, Z corrected for ties $= -1.832$, NS). Figure 3.8 gives the percentage of estimated births/conceptions per half month for the combined populations.

Table 3.12 Calculated median and mean birth/conception dates and associated standard deviations (SD) and standard errors (SE) for two donkey populations.

Population density	n	Median date	Mean date	SD (days)	SE (days)
High	60	October 10	November 10	31.72	4.10
Low	44	November 26	November 21	37.97	5.72
Both	104	October 10	November 12	35.23	3.45

The reproductive status of sampled females is described in Figure 3.9. The percentage of mature females that were pregnant was 87 percent in the high density population and 77 percent in the low density population. These proportions

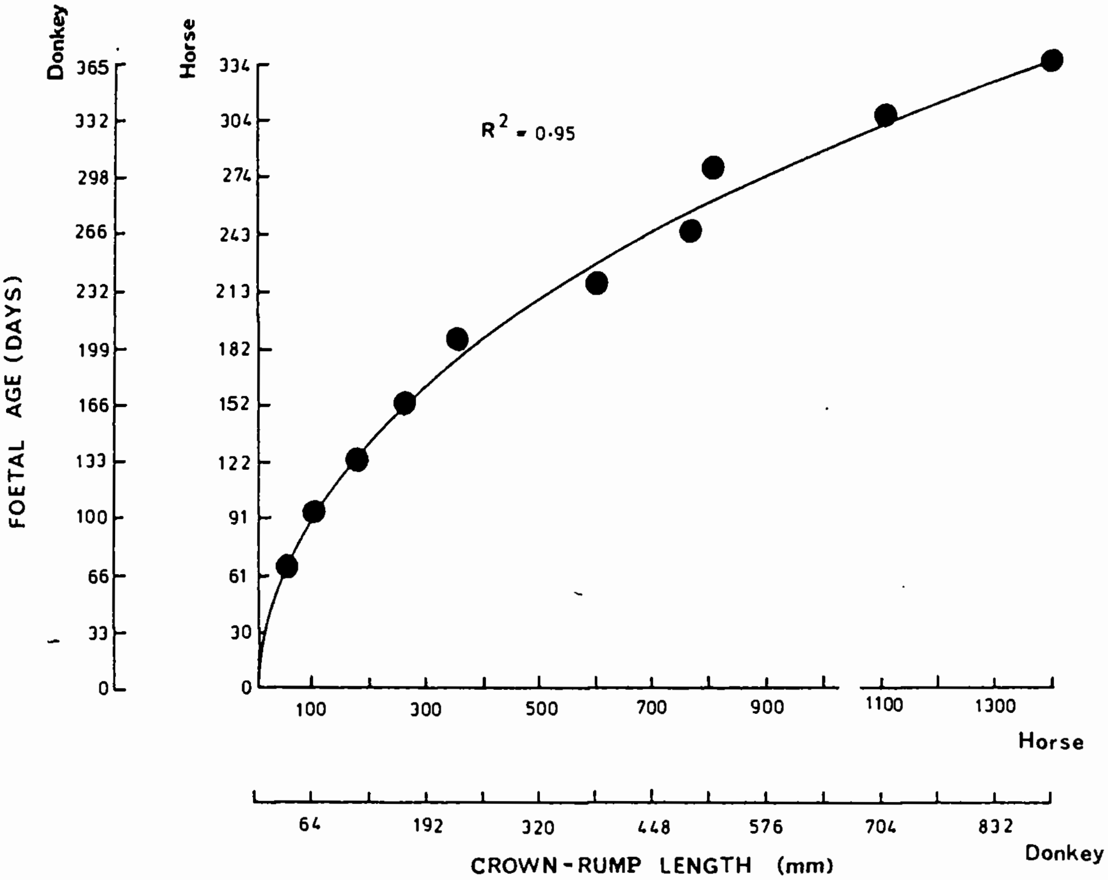

Figure 3.7 Relationship between crown-rump length (mm) and age for foetal horses derived from values given by Fraser (1971). The relatioship has been adapted for donkeys by adjusting size and age scales to appropriate values for donkeys using ratios given in McCool <u>et al.</u> (1981).

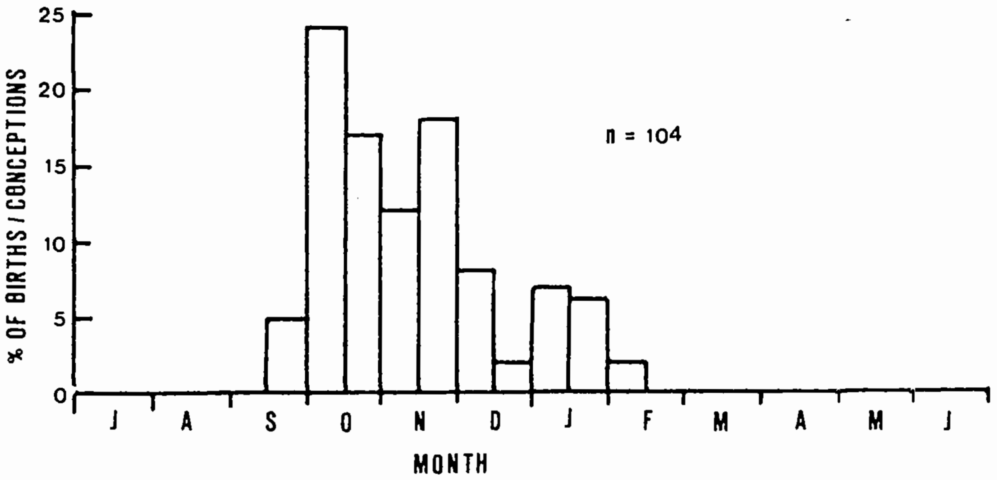

Figure 3.8 Percentage of births/conceptions occuring in half monthly intervals for both populations combined.

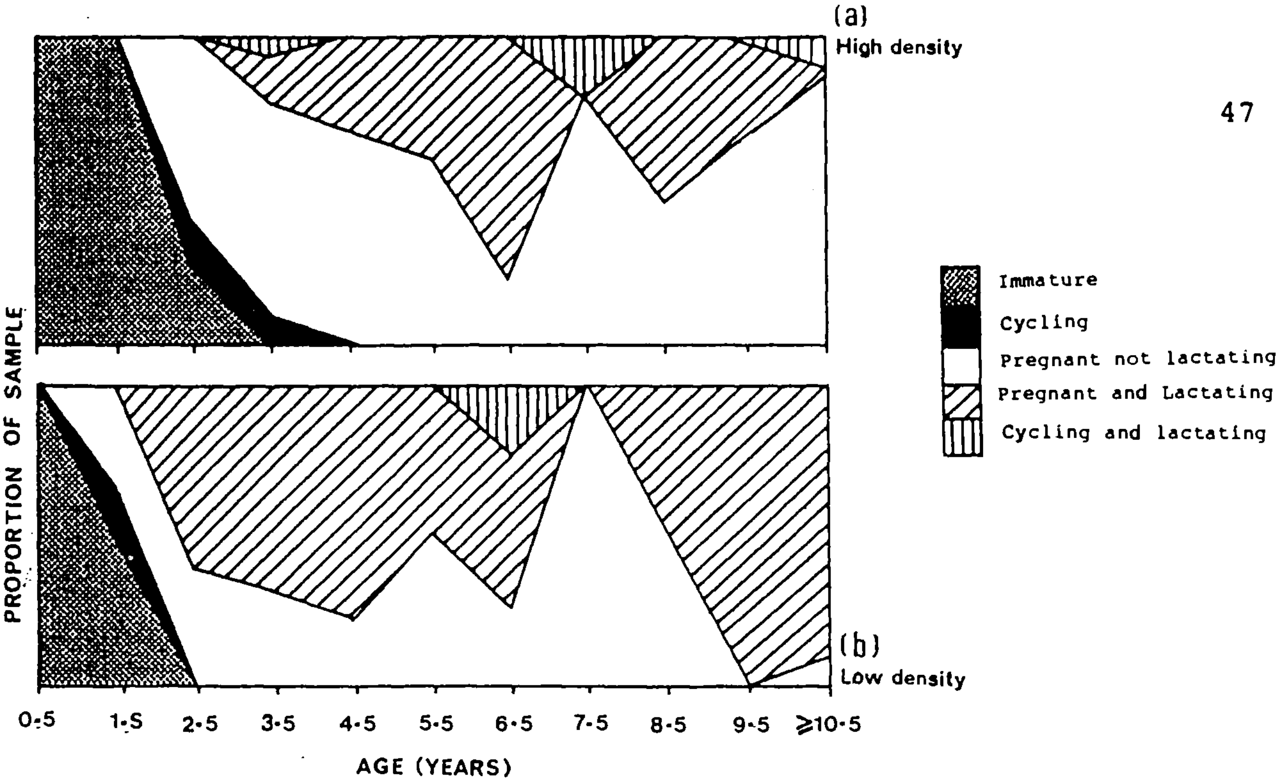

Figure 3.9 The proportion of females in each age class occurring in the given categories of reproductive status in the high (a) and low (b) density populations.

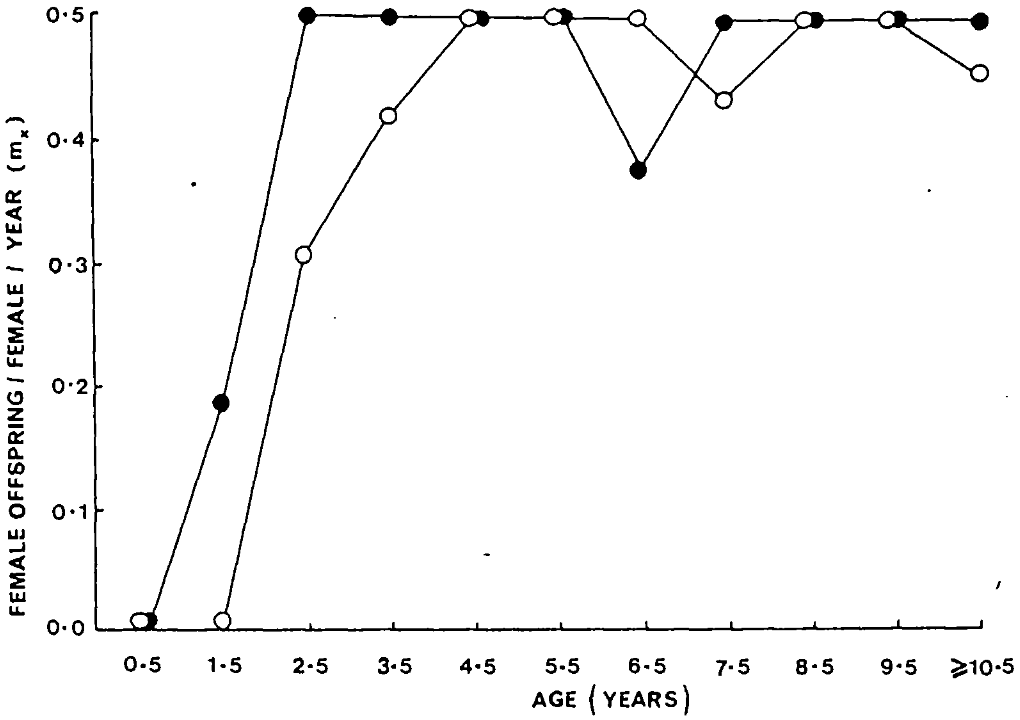

Figure 3.10 Age specific female fecundity measured as the number of female offspring produced per female per year (m_x), derived from the frequency of pregnant females in the high (O) and low (●) density populations.

were not significantly different (X^2 = 1.34, NS). The age specific fecundity was calculated as an m_x schedule, the number of female offspring produced per female per year at age x, calculated from the proportion of pregnant females in each age class. Figure 3.10 shows the m_x schedule for each population. As in males, female donkeys in the low density population appear, on average, to attain sexual maturity at a younger age than do females from the high density population. To test these differences, the observed frequency of pregnant females in each age class from each population was compared with an expected even distribution between populations. No significant departures from the expected even distribution were detected (Table 3.13).

Table 3.13 Tests for age specific differences in the fecundity of females (measured as m_x), at high and low population density. Observed frequencies of pregnant females are compared to an expected even distribution between populations. Test statistics (dependent upon sample sizes) are *Chi-square with Yates correction and, **Fishers exact probability test.

Age class	Test-statistic	p
1.5	0.20**	NS
2.5	0.21**	NS
3.5	0.52**	NS
6.5	1.00*	NS
7.5	1.00*	NS

Mortality

Sex ratios in standing age distributions were tested for significant departure from 1:1 in both populations (Table 3.14). No significant departures were evident, and hence male and female age class frequencies have been combined for further analyses.

Table 3.14 Tests for variation from a 1:1 sex ratio in age class frequencies for the a) high density and b) low density donkey populations. Brackets ({ or [) indicate that these age specific samples have been combined for chi-square testing.

	(a) High density:			(b) Low density:		
Age	X^2	df	p	X^2	df	p
0.5	0.222	1	NS	1.000	1	NS
1.5	0.529	1	NS	1.190	1	NS
2.5	0.520	1	NS	0.067	1	NS
3.5	3.024	1	NS	0.333	1	NS
4.5	1.118	1	NS	0.333	1	NS
5.5	0.091	1	NS	{ }		
6.5	0.400	1	NS	{ 0.402 }	1	NS
7.5	0.091	1	NS	{ }		
8.5	{ }			[ ]		
9.5	{ 0.587 }	1	NS	[0.323]	1	NS
$\geq$10.5	{ }			[ ]		

The exponential rate of increase in each donkey population was calculated from the 1986-87 survey results to be r = 0.0 for the high density population, and r = 0.18 for the low density population (Figure 3.2 and Table 3.1). The functions used to smooth the f_x series and track the temporal age distribution in the two populations were; for the high density population:

$$\text{Probit } (0.0216\ f_x) = 7.084 - 0.306x^{0.9}$$

and for the low density population:

$$\text{Probit } (0.0286\ f_x e^{0.18x}) = 5.753 - 0.152x^{0.8}$$

These functions were used to generate life-tables for the two populations, the age specific values for which are shown in Figures 3.11 a), b) and c). The two probit functions were also used to generate statistics describing the general properties of each life-table (Table 3.15) (Caughley 1970, 1976, 1977 p.97). The obvious differences between the life-tables calculated for the two populations are the much higher rate of foal (<0.5 year) mortality and the younger median age at adult death experienced by the high density population (Figure 3.11 and table 3.15).

Table 3.15 Summary of life tables calculated for the two donkey populations. Parameters are exponential rate of population increase (r), median age of adult deaths (M), standard deviation of adult ages at death (S), and adult mortality index of skew (Sk) (Caughley 1970, 1976, 1977).

Density	r	Mortality rate to age = 0.5	M	S	Sk
High	0.0	0.62	8.43	7.06	0.105
Low	0.18	0.21	7.39	9.71	0.223

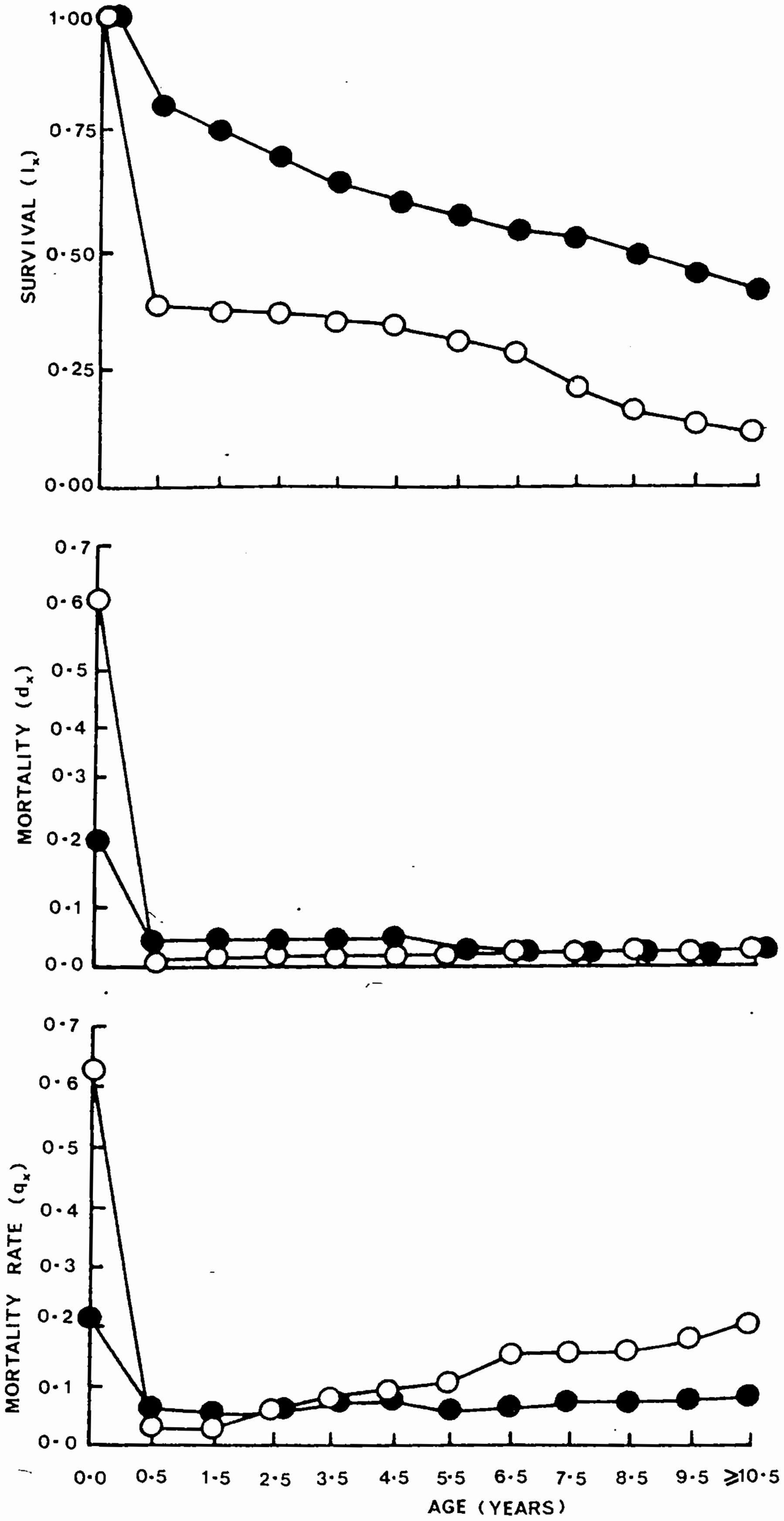

Figure 3.11 Age specific (a) survival (l_x), (b) mortality (d_x) and (c) mortality rate (q_x) of populations at high (O) and low (●) population density.

The use of standing age distributions to generate life-tables is valid only when the rate of population increase has been constant for some time, and hence the population age distribution is stable (Caughley 1977 p.95). The assumption that the high density population has maintained a zero rate of increase is valid given that the population has never been subjected to control. The low density population has not been subjected to control since 1983, and hence the observed rate of increase (r = 0.18) should have been constant for at least two generations. This approximates conditions Caughley (1977) sets as appropriate for use of the technique.

3.4 DISCUSSION:

Testing the food hypothesis

Caughley (1976) defines a model of ungulate population dynamics as an interactive ungulate-vegetation system. In the model, regulation of ungulate population abundance conforms to the food hypothesis, population abundance being ultimately limited by the food resources (vegetation) available to it. The model proposes that an ungulate population with a growth rate at or near zero will be at equilibrium density, and will be food stressed through high competition for available resources. In contrast an ungulate population reduced below equilibrium density will not be subjected to the stress of food shortage and will therefore have a high rate of increase. The proximate cause of differences in the rate of population increase between these populations would be density dependent variation in demographic traits related to the different nutritional stresses each population is subject to.

The only potential predator of donkeys in northern Australia is the dingo or wild dog (Canis familiaris dingo). This study supported the finding of McCool et al. (1981a) that there was no evidence consistent with dingo or dog predation upon donkeys in this region, and it was more probable that donkey populations were regulated by available food resources than by predation. Hence donkey populations were likely to conform to the food hypothesis and fit Caughley's (1976) ungulate-vegetation model.

Neither of the donkey populations examined in this study were subjected to significant culling before 1982. Both populations were at a high density (>10 donkeys per km^2), presumably at or close to equilibrium density in 1981 (Graham et al. 1982). Between 1982 and 1983 the Delamere population was heavily culled and its donkey population severely reduced. This low density population has not been culled since 1983 and should, according to the food hypothesis, be increasing in size back toward equilibrium density. The Coolibah population has never been culled and so should still be at or close to equilibrium density. The ungulate-vegetation model (Caughley 1976) predicts that the high density donkey population will be food stressed, while the low density donkey population will not. Further, that demographic rates will differ between the two populations giving the high density population a rate of increase close to zero while allowing the low density population to generate a positive rate of increase.

Rates of increase measured in each population between 1986 and 1987 (Figure 3.2 and Table 3.1) support the contention that the high density population is close to equilibrium density, while the low density population is increasing back toward equilibrium. The low density population was around half the size of the high density population in 1986, and increased by 20 percent (r = 0.18) in the subsequent 12 months. In contrast, there was no significant change in the size of the high density population (r = 0.0) between 1986 and 1987. Rate of increase measured in the growing population was close to that reported in Section 2 for other populations in northern Australia (r = 0.21).

Growth rate and body condition were measured in each population to determine whether they were subject to different levels of nutritional stress (Messier & Crete 1984). Growth rate represents an index of the long-term interaction of individuals and their environment (Hanks 1981; Skogland 1983). Maximum species-specific growth rate is probably genetically determined, but can be depressed by nutritional factors (Case 1978). Growth rates in the donkey populations examined in this study were dependent on population density. The high density donkey population did not attain its potential maximum rate over the first 3.5 years of life (Tables 3.5 & 3.6), presumably due to nutritional constraints (Case 1978).

Physiological body condition, like growth, characterises the interaction between an individual and its environment, but body condition provides an index to the short-term responses of individuals to prevailing environmental conditions (Hanks 1981; Shepherd 1987). In this study average body condition of donkeys at high population density was significantly depressed relative to their counterparts at low density (Figure 3.5).

Relative decreases in growth rate and/or body condition can be related to nutritional stress associated with fluctuations in food resources (Verme & Ozoga 1980a,b; Robbins & Robbins 1979; Blaxter & Hamilton 1980; Skogland 1983; Caughley 1987; Fryxell 1987), or changes in the abundance of animals competing for given food resources (Caughley 1970; Sinclair 1977; Skogland 1983). The food hypothesis predicts that evidence of nutritional stress will occur in populations at or close to equilibrium density. The density dependence of growth rate and body condition in donkeys suggests that nutritional stress occurs at high population density, and supports the prediction that a decrease in competition for food at lower population density has led to an alleviation of nutritional stress.

These findings provide strong evidence that donkey populations in northern Australia are extrinsically regulated by available food resources, and hence conform to the food hypothesis (Caughley 1976; Sinclair *et al.* 1985). The food hypothesis predicts that density dependent resource limitation in donkey populations will be reflected in density effects on demographic rates, particularly rates of mortality; and through them, on the rate of population increase (Caughley 1970, 1976; Sinclair 1975, 1977; Skogland 1985, 1986; Fryxell 1987).

Food limitation in the seasonally dry tropics

Sinclair (1975, 1977) studied the regulation of large, herbivorous mammal populations in the tropical grasslands of east Africa. He postulated that the rapid decline in the quantity of quality food at the beginning of the dry season was the main feature affecting the availability of resources to populations of herbivorous mammals. He pointed out that during the dry season, available food was often less than that required to maintain the herbivores feeding upon it, and that at such times the amount of available forage was low enough that it could be affected by the density of grazing herbivores themselves. Further, he suggested that food limitation during the dry season would lead to depression of body condition amongst herbivores, severe enough to adversely effect demographic rates. Hence, density dependent population regulation was mediated through density dependent changes in demographic rates arising from food shortage during the unproductive dry season (Sinclair 1975, 1977; Sinclair et al. 1985).

As with herbivore populations in tropical east Africa (Sinclair 1975, 1977), the quality and quantity of forage that would be available to donkey populations in northern Australia is highly seasonal. Vegetation growth is intimately associated with the annual wet and dry seasons (Mott & Tothill 1984). With the onset of rains between November and December there is a flush of nutrient rich pasture. Toward the end of the wet season in March and April, the nutrient quality of available pasture has fallen dramatically although the dry matter yield of the pasture may remain high for some weeks into the dry season. The annual cycle of vegetation growth and dieback produces alternating periods of superabundant and depauperate forage conditions which are both seasonally predictable and relatively reliable from year to year for resident herbivores (Mott et al. 1985; Tothill et al. 1985). According to the food hypothesis (Sinclair 1975, 1977; Sinclair et al. 1985), donkey populations are regulated by density dependent changes in demographic rates, mediated through food shortage during the dry season. The effects of this seasonally predictable cycle of forage quality and availability on rates of reproduction and mortality in donkey populations are examined in the following discusson.

The effect of density on demography

Although donkeys are poly-oestrous and hence capable of producing young throughout the year (Woodward 1976; Perryman & Muchlinski 1987), in northern Australia conception/birth is seasonal, peaking in the two months prior to the monsoonal wet season in October and November and ceasing by early February (Figure 3.8). This is in contrast to donkey populations in North America where breeding occurs throughout the year with no apparent seasonality (Moehlman 1974; Woodward 1976: Norment & Douglas 1977; Seegmiller & Ohmart 1981; Johnson et al. 1987; Perryman & Muchlinski 1987). Thus in northern Australia, donkey reproduction is facultatively seasonal, occuring at the end of the dry season, the time of year when females will presumably be in the poorest condition. However, the onset of the wet season at the begining or soon after the birth pulse would associate the annual flush of quality forage with lactation. In terms of energy, lactation is the most costly component of reproduction for female mammals (Sadlier 1972).

The ability of mammals to maintain adequate supplies of milk has consequences for postnatal development and survival of offspring (Thorne et al. 1976; Blaxter & Hamilton 1979).

The coincidence of lactation with the period of maximum potential resource accumulation by females would appear therefore, to be advantageous for both females and their offspring (Rutberg 1987). The lack of a seasonal breeding pattern in north American donkey populations may be related to the absence of seasonally marked climatic variation in the regions they occupy. Feral donkey populations in North America are restricted to the largely semi-arid areas of the western half of the continent (McKnight 1964), which lack the predictable season of rainfall and vegetation growth which characterise northern Australian grasslands. Rutberg (1987) suggested that under conditions of little or no seasonal climatic variation, reproductive seasonality would become progressively less marked in food-limited mammal species.

Because female donkeys in northern Australia breed just prior to the wet season, they must maintain sufficient condition through the previous dry season to allow them to reproduce. Fecundity in northern Australian populations was high and independent of population density with more than 75 percent of mature females breeding each year (Figures 3.9 & 3.10). This means that wet season food supply must be substantial enough that donkeys, even at equilibrium density, do not reduce their available forage to a point where female body condition is sufficiently depressed to adversely affect reproduction at the end of the subsequent dry season.

Fecundity in northern Australian donkey populations is maintained at a high level, independent of population density due, it appears, to the annual super-abundance of forage each wet season (Tothill et al. 1985). However, during the dry season, forage becomes limiting and although depletion of quality forage over the dry season has no impact on fecundity, density dependent food limitations would be expected to exert strong influences on rates of mortality (Caughley 1970; Sinclair 1977; Skogland 1985; Fryxell 1987).

Age specific mortality in donkey populations did not differ between sexes. It conformed to the general pattern described for mammals by Caughley (1966). High mortality amongst juveniles was followed by a period of low mortality through middle ages, with an increasing mortality rate through later ages (Table 3.15 & Figure 3.11). At high population density, juvenile mortality was pronounced, around 60 percent of foals dying in the first six months of life, in contrast with around 20 percent at low population density. Variation in the age of adult deaths was less at high density, conforming to Caughley's (1970, 1976) prediction that the distribution of age specific adult mortality at high population density will be constricted. However, the contention that the index of skew of the distribution of adult mortality with age should decrease as r increases (Caughley 1976), was not supported by the mortality schedules produced in this study.

Density dependent mortality over the first six months of life is clearly the most important demographic factor regulating population abundance in feral donkeys. Juvenile mortality has been identified as a primary factor influencing population growth in other ungulates (Caughley 1970, Grubb 1974; McCullough 1979; Sinclair 1979; Clutton-Brock, Major & Guiness 1985; Sinclair & Norton-Griffiths 1982; Sauer & Boyce 1983; Skogland 1985). Between birth and the mid-point of the first dry season, donkey foals at high population density are subjected to considerable mortality, almost three times that of donkeys in the low density population. The source of this mortality is unknown, but seems likely to be associated with inadequate supplies of milk to the foal and/or inability to obtain sufficient nutrients or energy from available forage following weaning. Juvenile donkeys from the high density population were in the poorest average condition of any donkeys sampled (Figure 3.5). The depletion of available forage in terms of both quality and quantity as the dry season progresses is a function of climate (Mott & Tothill 1984; Tothill <u>et al.</u> 1985). Hence, the quality of diet available to donkeys at both high and low population density would be reduced through the dry season. This will have consequences for both the ability of females to maintain lactation beyond the vegetation flush of the wet season and the ability of foals to obtain a diet sufficient to survive through the dry season.

The food hypothesis (Caughley 1976; Sinclair 1975, 1977) predicts that at high population densities, increased competition for available forage would accelerate depletion of favoured forage species, leading to additional nutritional stress for young donkeys relying on their mothers for milk or attempting to extract a sufficient diet from dry season vegetation. This study suggests that additional nutritional stress through competition for food at high density is enough to increase donkey mortality over the first six months of life by nearly 200 percent at high population density.

Adult mortality rate also increased at high population density, particularly amoungst the oldest individuals (Figure 3.11). Similar responses have been observed in other food limited ungulate populations (Caughley 1970, 1976; Podoler & Rogers 1975; Sinclair 1977, 1979; Clutton-Brock _et al._ 1985; Sinclair _et al._ 1985; Fryxell 1987). However the role of adult mortality in regulating donkey population abundance is clearly less influential than is mortality over the first year of life.

This study suggests that feral donkey populations in northern Australia are ultimately regulated by food resources and proximally by density dependent changes in mortality rates. Like other large, herbivorous mammal species, donkeys conform to the food hypothesis being regulated through food limitation (Caughley 1970, 1976; Sinclair 1975, 1977; McCullough 1979; Fowler 1981; Houston 1982; Sinclair *et al.* 1985).

Section 4:

MODELLING THE COST OF POPULATION CONTROL

4.1 INTRODUCTION:

When planning pest control programs, a useful early step is the systematic assessment of the balance of benefits and costs. Although benefit/cost analyses are common in programs to control invertebrate pests (Conway _et al._ 1975; Conway 1981), such analyses are rarely attempted for programs to control vertebrate pests (Caughley 1977, p.204). Given the large scale of many vertebrate pest control operations (eg: Child _et al._ 1970; Newsome _et al._ 1972; Parkes 1984; Davis 1986; Bayliss & Walsh 1987), some assessment of the potential costs involved would seem a responsible requirement.

Recently, control of feral donkeys has been attempted in several areas of northern Australia where they are considered to compete with domestic stock for feed, cause significant pasture degradation, and represent a potential vector for the spread of exotic livestock diseases (Wheeler 1987; Wilson 1987). One such exercise carried out in the Victoria River District, was discussed in Section 2. While the immediate reduction of donkey abundance in these areas was the primary aim of these control exercises, ongoing restraint of donkey populations at manageable densities is a desirable longer-term objective (Letts et al. 1979). In order to conduct benefit/cost analyses, appraise various control strategies and forecast resource requirements for feral donkey control, it was considered important to estimate the potential costs of ongoing population control.

Benefit/cost analyses of invertebrate pest control usually involve identification of the population size which maximises the benefits of control by balancing the marginal costs incurred by control, and marginal returns from control (Headley 1972). This population size is derived from an economic threshold model such as that described by Headley (1972). These models include some function of the cost of controlling a pest population at given levels of abundance. Cost of control functions assume that the cost of controlling a population at given population sizes is continuous, increasing as the population is held at progressively lower densities and that costs increase at a accelerating rate. Headley (1972) models this function as a hyperbola, but makes no attempt to identify or define components contributing to its shape. Recently, economic threshold models have been used to examine the relative costs and benefits involved in the control of two vertebrate pests, feral pigs (*Sus scrofa*, Tisdell 1982) and prairie dogs (*Cynomys ludovicianus*, Collins et al. 1984). In both cases estimates of either the rate of population increase or the rate of repopulation were incorporated into functions describing the costs of ongoing population control. However, factors influencing these cost functions remain poorly defined and hence difficult to incorporate into numerical benefit/cost analyses (Tisdell 1982).

This section reports the results of a study undertaken to derive numerical models of the relative cost of the long-term control of feral donkey populations. Components of these models are identified, estimated and then used to derive cost of control functions. The utility of the models are demonstrated by using them to compare the relative expense of two control strategies.

The cost of population control

An animal population reduced to some level of abundance (N_C) which is below its equilibrium density (K) generates a positive annual exponential rate of population increase (r). The number of animals added to the population each year when r is positive is the population's annual productivity (HN). If N_C is considered an acceptable level of abundance for a population of pests, following the reduction of the population to N_C, HN must be removed from the population annually to restrain it at N_C (Tisdell 1982). The overiding determinant of r (and hence HN) for most vertebrate populations is the prevailing density of the population itself (Caughley 1976). Density-dependence of r has been the subject of considerable research, and several models describing how r varies with prevailing population density have been formulated (eg: Andrewartha & Birch 1954; Ricker 1958; Leslie 1959; Caughley 1976). One of the simplest of these models, and the one used in this study to estimate HN for donkey populations at given N_c, is the logistic (Caughley 1976). The logistic model is most commonly associated with populations at the first trophic level and may consequently appear an overly simple way of viewing donkey population growth. Because donkey populations in northern Australia are regulated by food resorces (Section 3), a productivity model that considered the interaction of donkeys with their food supply would provide a more appropriate description of population growth than the logistic model used here (Caughley 1976; Caughley & Lawton 1981). However, not enough is known about the interaction of donkeys with their food resources to estimate the parameters necessary to derive an interactive model of population regulation (Caughley 1976). Hence, a logistic model is used here to give a first approximation of donkey population growth, in order to provide insights into the role of population productivity in long-term population control.

A logistic model of feral donkey population growth is derived and used to estimate the number of donkeys that have to be removed to reduce a donkey population from K to N_c, and then the number of donkeys that must be removed annually to restrain the population at N_c. To attach some measure of the cost incurred by removing each donkey, the relationship between the cost per donkey removed and the prevailing population density is examined and modelled.

Agents used to control pest populations are analagous to predators consuming prey (Hone 1986). As such, classical predator-prey theory is useful in modelling functional relationships between pest density and the effort expended to remove them. The rate at which a predator consumes prey is a function of the prevailing density of prey (Holling 1959; Taylor 1984). The form of the relationship between the predation rate (prey consumed per predator per unit time) and prey density is generally a monotonic function where saturation of predation rate is approached asymptotically as in Holling's (1959) functional response curves (Figure 4.1a). Predation rate increases with increasing prey density because the time that a predator has to spend searching for a prey to consume (search time) decreases as the number of prey available to be found increases. The rate of increase in predation rate slows and then stops as search time decreases to the point where it is negligible compared to the time taken to consume each prey once it has been found (handling time). At this point predation rate becomes a constant representing handling time alone, and further increases in prey density elicit no further increases in predation rate (Holling 1959; Taylor 1984).

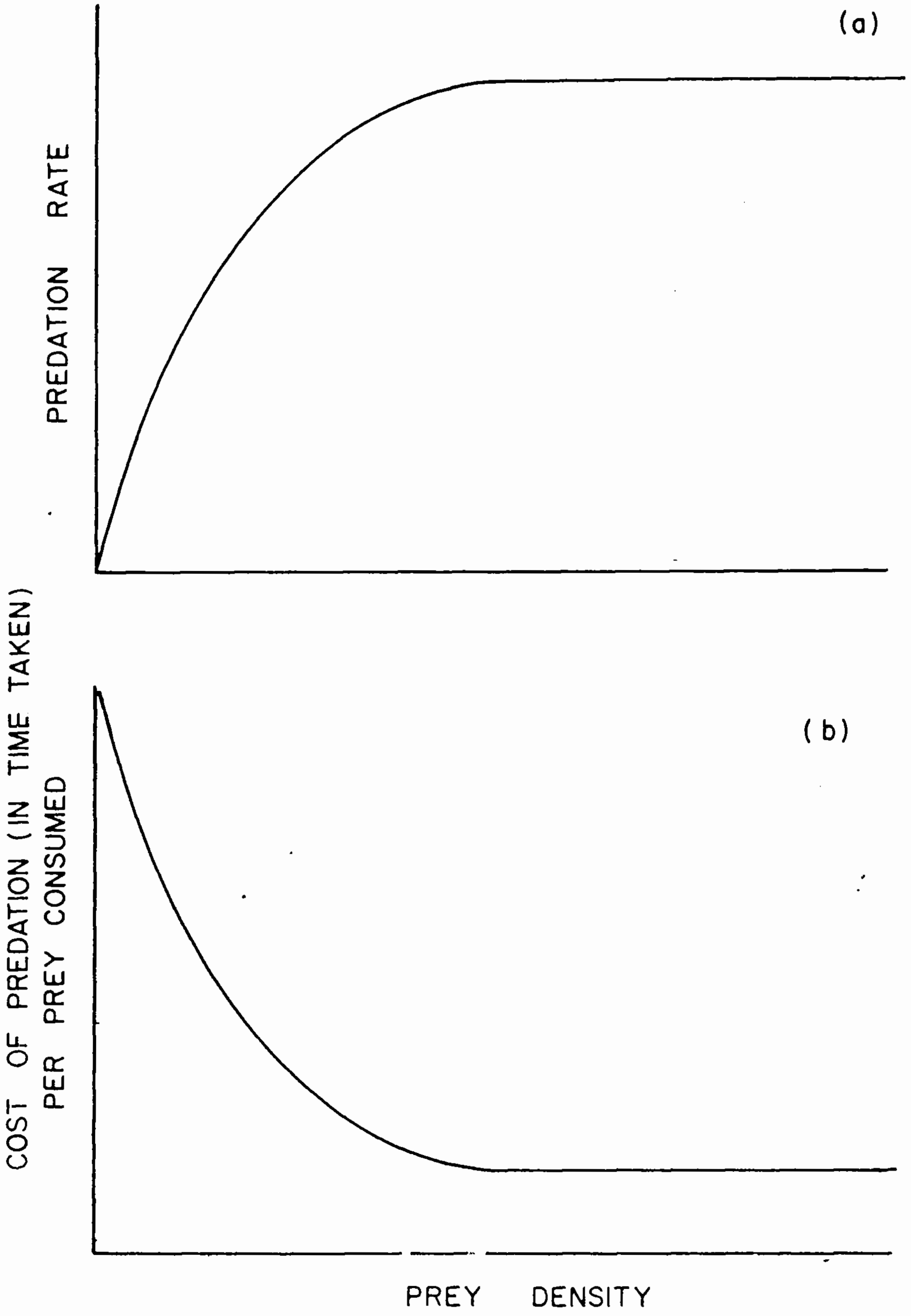

Figure 4.1 (a) Holling's (1959) Type II functional response curve describing changes in predation rate (prey consumed per predator per unit time) with increasing prey density.

(b) The relationship of the cost of predation measured as time taken per prey consumed, with increasing prey density. The curve is the inverse of Holling's Type II functional response.

The two components of time that determine predation rate constitute the "cost" of predation to the predator. This cost measured as the time expended per prey consumed will be the inverse of predation rate, and when considered in terms of prevailing prey density will form an inverted functional response curve (Figure 4.1b). Hence in functional control terms, the cost per pest (prey) removed from a population (consumed), measured as the amount of time taken to remove each pest, decreases with increasing pest density to a point where the time spent searching for pests becomes negligible compared to the time taken to physically remove each pest. At this point the cost per pest removed becomes a constant. The density of pests at this point represents a saturation pest density. Increases in pest density beyond saturation will offer no further decrease in the amount of time taken per pest removed.

In this Section these two density-dependent relationships, population productivity and the cost per pest removed, are estimated for feral donkeys as numerical functions. The two functions are then combined to predict the cost of ongoing control of feral donkey populations.

4.2 METHODS:

Modelling population productivity

A logistic model describing population productivity (HN) for prevailing population size (N) is:

$$HN = r_m N (1 - N/N_K) \qquad (1)$$

where r_m is the intrinsic exponential rate of population increase and N_K is the size of the population at equilibrium density, K (Caughley 1977, p.179). HN was estimated for feral donkeys assuming an arbitary population size of 1,000 at K. Section 2 estimates r_m for feral donkeys in northern Australia, and this estimate is used here to construct a population productivity model.

Modelling the cost of donkey removal

The relationship between the cost per donkey removed and prevailing donkey density was determined for donkeys being shot from helicopters, the standard technique employed for donkey control in northern Australia (Wheeler 1987; Section 2). An area of 5,128 km^2 in the north of the Victoria River District, which contained significant donkey densities was surveyed from the air to determine the initial (pre-shooting) density distribution of the donkeys. Details of the survey techniques and variables used are given in Bayliss (1985a) and Section 2.

The area was divided into 5x5 km cells and a donkey density (donkeys per km^2) assigned to each cell. A smoothed donkey density distribution was mapped for the area. Donkeys were shot from helicopters over 12 days. Shooting was concentrated daily in cells containing similar densities of donkeys according to the mapped density distribution, progressing from cells with the highest pre-shoot donkey density on day one, through to cells with progressively lower donkey densities on subsequent days. On the first occasion that a cell was shot, the amount of time spent flying over the cell was divided by the number of donkeys shot in the cell to give a measure of the amount of flying time expended per donkey removed (hours per donkey removed) from the cell. This measure was averaged across cells shot for the first time on each day and relationships were developed between hours per donkey removed and the average pre-shoot donkey density in cells shot on each day derived from the mapped donkey density distribution. Hours of flying time was used throughout this study as an index of the cost of donkey removal and hence ultimately the cost of population control. Helicopter charter is by far the major component of cost involved in feral donkey control and hence provides a precise index to the overall cost of control operations.

In order to relate the population productivity model to the model predicting the cost per donkey removal, the arbitary population of N_K = 1,000 had to be associated with some estimate of equivalent population density. To do this an estimate of the equilibrium population density (K) of donkeys was required. K was estimated by averaging the individual cell densities used to construct the donkey density distribution. Because K represents the density of donkeys at ecological carrying capacity (Caughley 1979), it was considered appropriate to restrict calculation of K to cells containing significant densities of donkeys (ie areas containing the highest homogenous donkey density). Hence only cells containing densities of more than 2 donkeys per km^2 were used in the calculation of K.

4.3 RESULTS:

Population productivity

The annual exponential rate of population increase (r_{obs} = 0.21) for feral donkey populations in northern Australia recovering following reduction for control is estimated in Section 2. It has been demonstrated that r_{obs} for a substantially reduced population of food limited animals should coincide with the intrinsic rate of population increase, r_m (Caughley 1976; Caughley & Krebs 1983). Figure 4.2 shows how the logistic model predicts population productivity will vary with population size for feral donkeys, assuming a population size of 1,000 at K and an r_m of 0.21.

In terms of population control, the initial population size (assumed here to be the size of the population at equilibrium density, N_K) must be reduced to the acceptable or controlled population size N_c. Annual reduction to restrain the population at N_c following initial reduction from N_K will simply be HN for a population size of N_c.

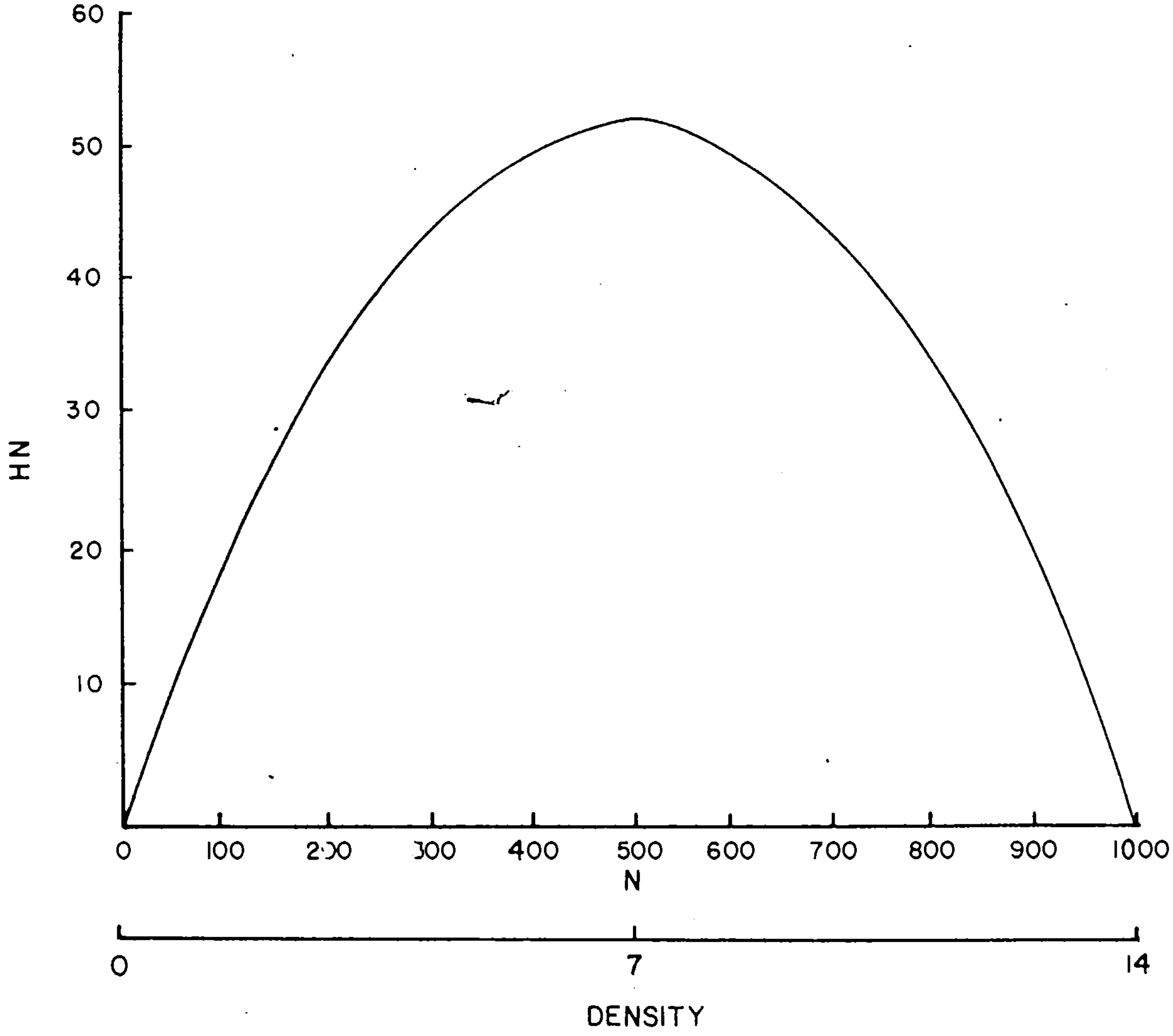

Figure 4.2 Population productivity (HN) as a function of population size (N), assuming an equilibrium population size (N_K) of 1,000 and logistic population growth. The secondary abscissa gives population densities (donkeys per km^2), assuming an equilibrium population density (K) of 14.

Donkey density averaged across cells containing densities greater than 2 donkeys per km^2 was 14 donkeys per km^2. This was taken as an estimate of the equilibrium density (K) for donkey populations. A secondary abscissa in Figure 4.2 shows the association between population density and HN.

The cost of removing donkeys

Various curvilinear models could be fitted to the observed relationship between population density and the average cost per donkey removal. An inverted Michaelis-Menten saturation curve (Noy-Meir 1978) and a simple Ramp model are examined here.

The Michaelis-Menten saturation function has been used extensively to model predator-prey interactions (Real 1977 and references therein), and is described by:

$$C = 1 - \left[-a + c\left(\frac{d}{d + D}\right) \right] \qquad (2)$$

where C is the average cost per animal removed and d is the prevailing animal density (animals per km^2). The coefficient c is the rate at which the maximum rate of decrease in C, a, is ameliorated by increasing animal density. D is a measure of the relative efficiency of the removal function, the higher the value the lower is the relative efficiency.

Coefficients for the model were estimated by converting equation (2) into linear form (Bayliss 1985b) and reducing residual variance about the least squares line of best fit by iteration of the coefficient a. The linear form is:

$$\left(\frac{1}{C + a}\right) = \frac{1}{c} + \frac{D}{c} \cdot \frac{1}{d} \qquad (3)$$

No significant improvement in the fit of the linear model was obtained beyond a value of -0.89 for coefficient a. Model coefficients were derived from the significant intercept ($t = 18.57$, $p < 0.001$), and slope ($t = 4.93$, $p < 0.001$) of the line of best fit ($R^2 = 0.71$). The modelled relationship is described by:

$$C = 1 - \left[0.89 + 0.10 \left(\frac{d}{d + 1.27}\right)\right]$$

The Ramp model describes a linear relationship between the decrease in cost per donkey removal and donkey density to the point where cost per removal is saturated. A linear regression was fitted through the 'ramp', and the intercept used to calculate the maximum cost of donkey removal. The slope of the regression line gives the rate of decrease in cost per removal as higher donkey densities are encountered. The saturated (asymptotic) cost per removal was estimated from the mean of points falling above saturated density, arbitarily chosen to be 5 donkeys per km^2. The model is described by:

If $d < 5$ donkeys per km^2:

$$C = 0.06 + (-0.01\ d)$$

If $d > 5$ donkeys per km^2:

$$C = 0.018$$

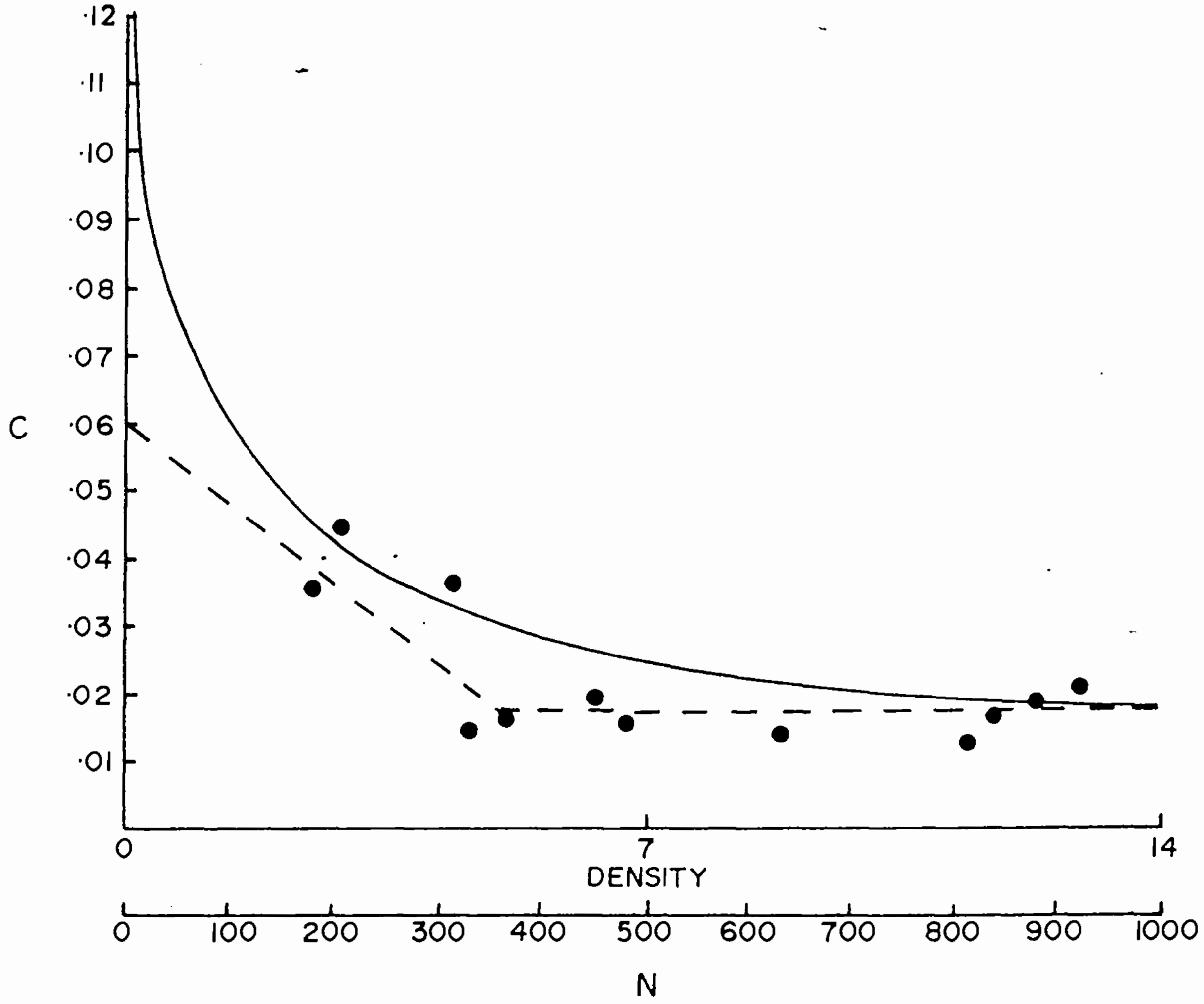

Figure 4.3 The predicted Michaelis-Menten (——) and Ramp (- - -) functions decribing the relationship of average cost per donkey removed measured as hours of helicopter time per donkey killed (C), on average prevailing donkey density (donkeys per km^2) for 12 days of shooting. The secondary abscissa is the corresponding size of a population of 1,000 donkeys at equilibrium density (K).

Both the inverted Michaelis-Menten and ramp models are illustrated in Figure 4.3. The Michaelis-Menten and ramp models both provide an adequate fit to the observed data. The Michaelis-Menten saturation curve has been chosen to represent the cost of removal function in all further modelling because its coefficients can be directly interpreted as components of the predator-prey analogy (Real 1977, 1979; Taylor 1984).

Modelling the cost of population control

The logistic model given in equation (1) and the cost of removal function given in equation (2) allow ongoing costs of population control to be calculated. Reduction of the population to the desired level of abundance (N_C) can be achieved in a variety of ways depending primarily upon how quickly control of the population is to be established. Two strategies for achieving population control were examined:

Strategy 1. Instantaneous reduction; where reduction to N_C is achieved in the first year of control by a large-scale reduction from N_K. The annual removal of HN is then the only requirement for ongoing restraint of the population at N_C.

Strategy 2. Proportional reduction; where a set proportion of the population (H) is removed in each year of control. The proportion of the population that must be removed can be pre-determined to stabilize the population at N_c by:

$$N_c = N_k - \left[\frac{N_K \cdot H_s}{r_m}\right] \qquad (4)$$

where H_s is the instantaneous rate of removal expressed as a proportion of the prevailing population size (after Caughley 1977, p.202).

Considering instantaneous reduction first, the cost of the initial reduction of the population from N_K to N_c (C_{red}) can be estimated by:

$$C_{red} = \sum_{i=1}^{F} 1- \left[-a + c\left(\frac{d - d_i}{d - d_i + D}\right)\right] \qquad (5)$$

where d is the original population density (equivalent to N_K), F is the specified control density (equivalent to N_c), and d_i is the density represented by the progressively reduced population where i is the change in population density equivalent to the number of animals removed. The cost of removing each animal must be recalculated as the population density is progressively reduced ($d - d_i$), and summed until the specified control density F is attained. At this point $d_i = F$ and $d - d_i$ will be the reduction in population density achieved. This progressive summing of costs is necessary as each subsequent removal reduces the

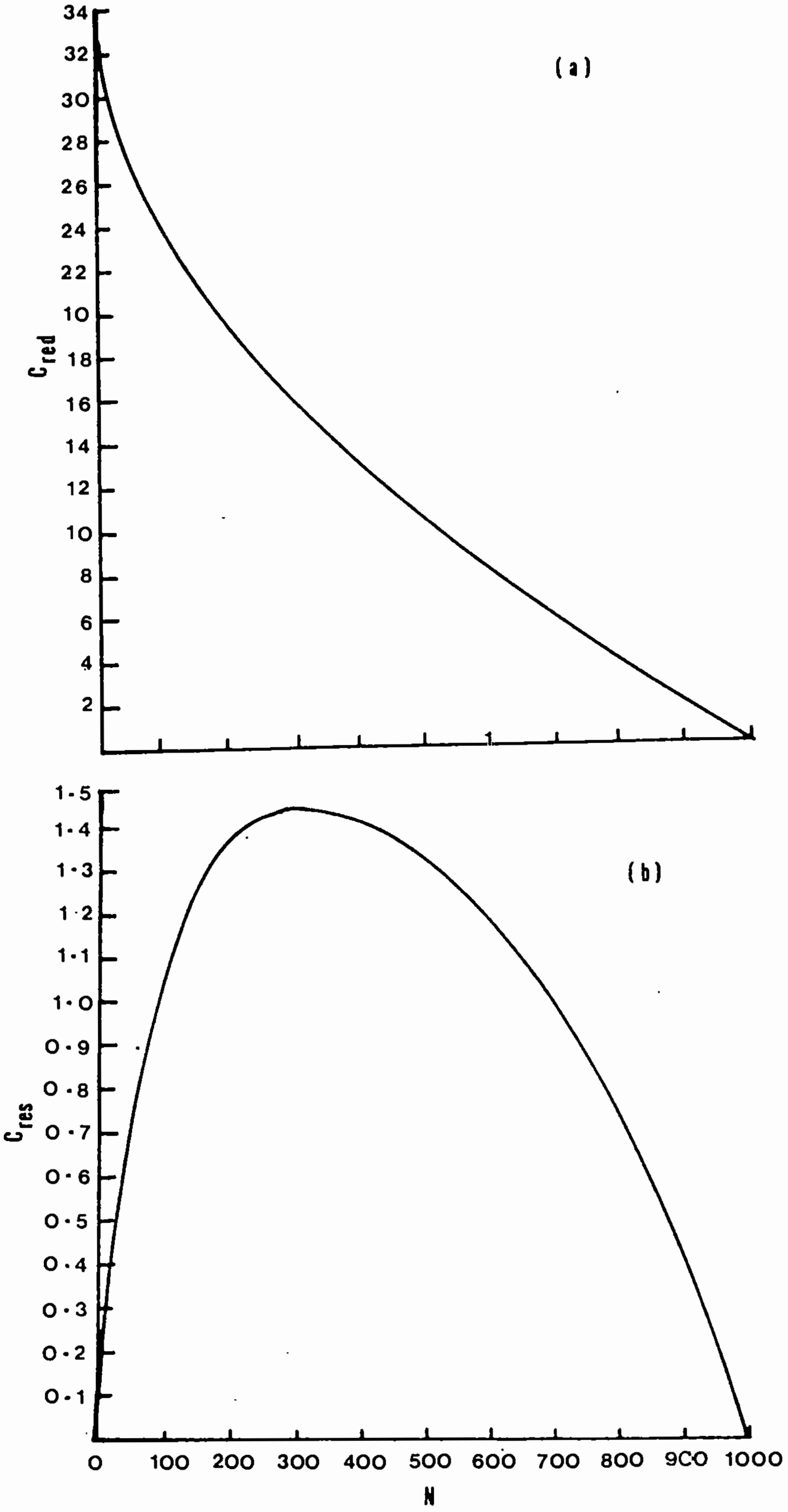

Figure 4.4 (a) The cost of initially reducing a population of 1,000 donkeys (C_{red}) at equilibrium density to a given control population size (N_c). C_{red} is the number of helicopter hours taken for the specified reduction predicted from the cost of removal model described in the text.

.(b) The annual cost of restraining a population donkeys (C_{res}) at a given control population size (N_c). C_{res} is the number of helicopter hours taken to remove the necessary number of donkeys to restrain the population at N_c.

prevailing population density, and hence increases the cost of the removal by a factor given by equation (2). For a population of feral donkeys where $N_K = 1,000$, the variation in C_{red} with specified N_C is shown in Figure 4.4a.

The cost of restraining a population at N_c (C_{res}) is the product of how many animals must be removed from the population annually to maintain control (HN) and the cost of each of these removals. C_{res} will depend upon whether animals are added to the population over the entire year (non-seasonal additions) or over a distinct part of the year (seasonal additions), and whether animals are removed over the entire year or over a distinct culling season. C_{res} varies because the cost of removing each animal changes with population density according to equation (2), and the prevailing density of animals varies over the year depending on the temporal pattern of additions to and removals from the population.

Feral donkeys reproduce seasonally in northern Australia (McCool <u>et al.</u> 1981a; Section 3). Hence, if a strategy of reducing the population outside of the breeding season is adopted; after initial reduction of the population to N_c is achieved, removal of HN involves reduction of the population from levels equivalent to N_c + HN. C_{res} can therefore be calculated by substituting density values equivalent to the population size before the removal of HN (calculated using equation (1)), and the progressively reduced population size as HN is removed; for the coefficients d and d_i respectively in equation (5). In this case d_i will equal the population density during the progressive removal of HN, until population size returns to N_c. For a donkey population of 1,000 at N_K, the expected changes in C_{res} with population size at N_c are shown in Figure 4.4b.

C_{red} and C_{res}, the two components of the overall cost of controlling a feral donkey population using the instantaneous reduction strategy, can be combined to predict the cost of controlling a feral donkey population at any level of N_c over any number of years. Figure 4.5 demonstrates by way of a response surface, how the cumulative cost of control varies for a donkey population of 1,000 at N_K. The response surface describes the cost of attaining N_c in year 1 of control and the accumulation of costs incurred through control of the population at 10 levels of N_c over 150 years. The year 1 starting points are equivalent to C_{red} given in Figure 4.4a, and the slopes of the lines describing the annual accumulation of control costs at the 10 levels of N_c considered, are equivalent to values of C_{res} as given in Figure 4.4b.

When proportional reduction is considered, the instantaneous harvest rate (H) required to stabilize the population of 1,000 donkeys at N_c (H_s) (equation (4)), and the number of years required to attain stability for given

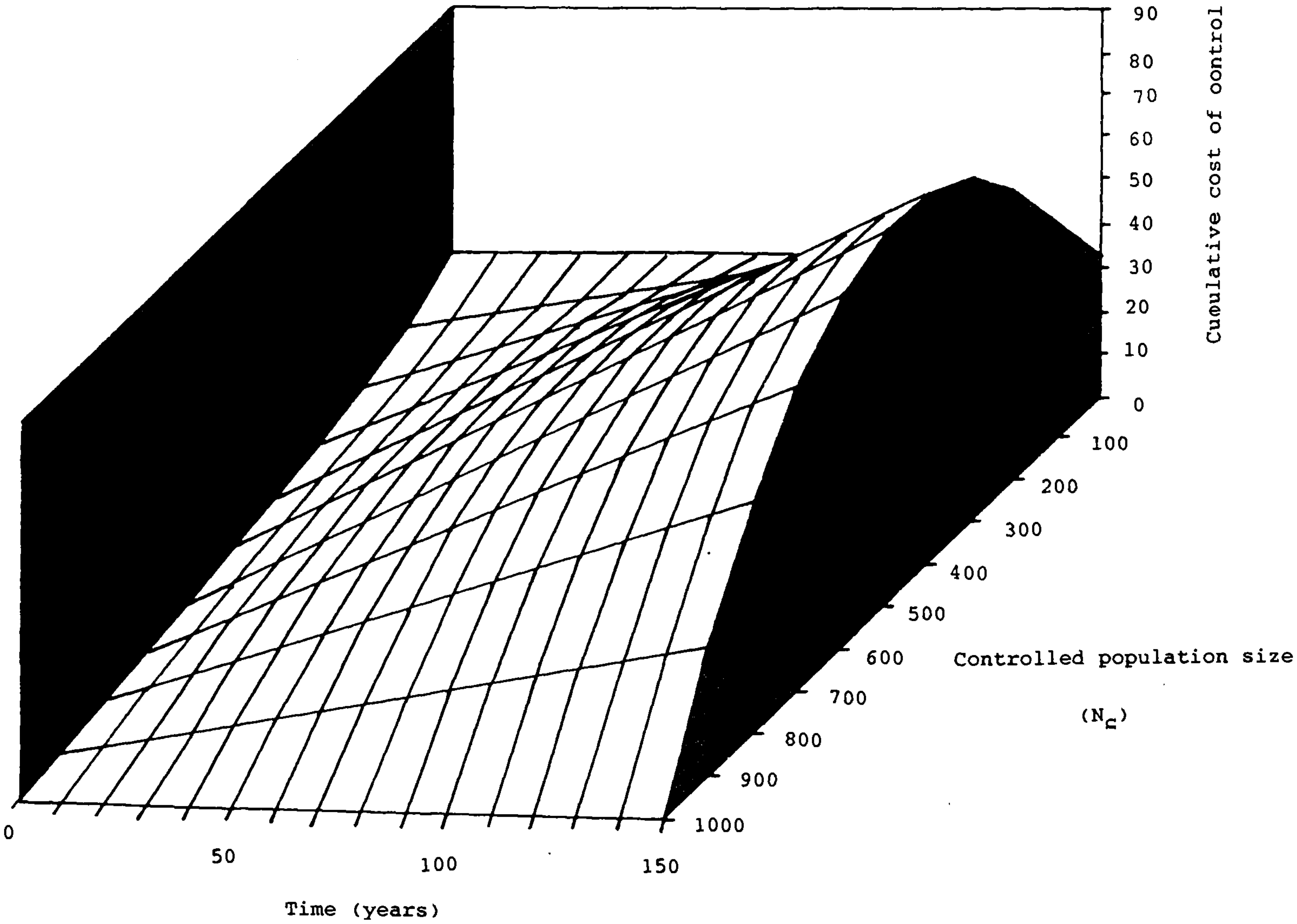

Figure 4.5 A response surface demonstrating variation in the cumulative cost of controlling a population of 1,000 donkeys at 10 controlled population sizes (N_c), over 150 years, using the instantaneous reduction strategy described in the text. Cumulative costs are measured as the accumulated helicopter hours required to achieve and maintain control. The initial population of 1,000 donkeys is assumed to be at equilibrium density.

H_s, is shown in Figure 4.6. The response surface shows how population size changes over 150 years under 10 different harvesting rates (H). If H is greater than 0.20 (assumed here to be the donkey populations intrinsic rate of increase), eradication of the population will be achieved (the stippled area in Figure 4.6). When H is less than 0.20, the population stabilizes at some level of N_c, indicated by the line of crosses on the response surface. In these cases H becomes H_s for given N_c, and as H_s increases N_c decreases to a point where $H_s = 0.20$ and $N_c = 0$. However, the time taken to stabilize the population at N_c increases markedly at high levels of H_s. As levels of H_s approach 0.20, stability at N_c is not attained within the 150 years which Figure 4.6 assesses. The cost of controlling the population by proportional reduction is given by:

$$C = \sum_{y=1}^{Y} \left\{ \sum_{i=1}^{H_s(d_y)} 1 - \left[-a + c\left(\frac{d_y - d_{iy}}{d_y - d_{iy} + D} \right) \right] \right\} \qquad (6)$$

where the cumulative cost of control (C) is assessed over a given number of years (Y) by accumulating the cost of proportional removal in annual increments (y). For each year, y, H_s is the instantaneous rate of harvest that will ultimately stabilize the population at densities equivalent to N_c, d is the density of the unculled population and d_i is the density of the progressively reduced population where i is the change in population density equivalent to the number

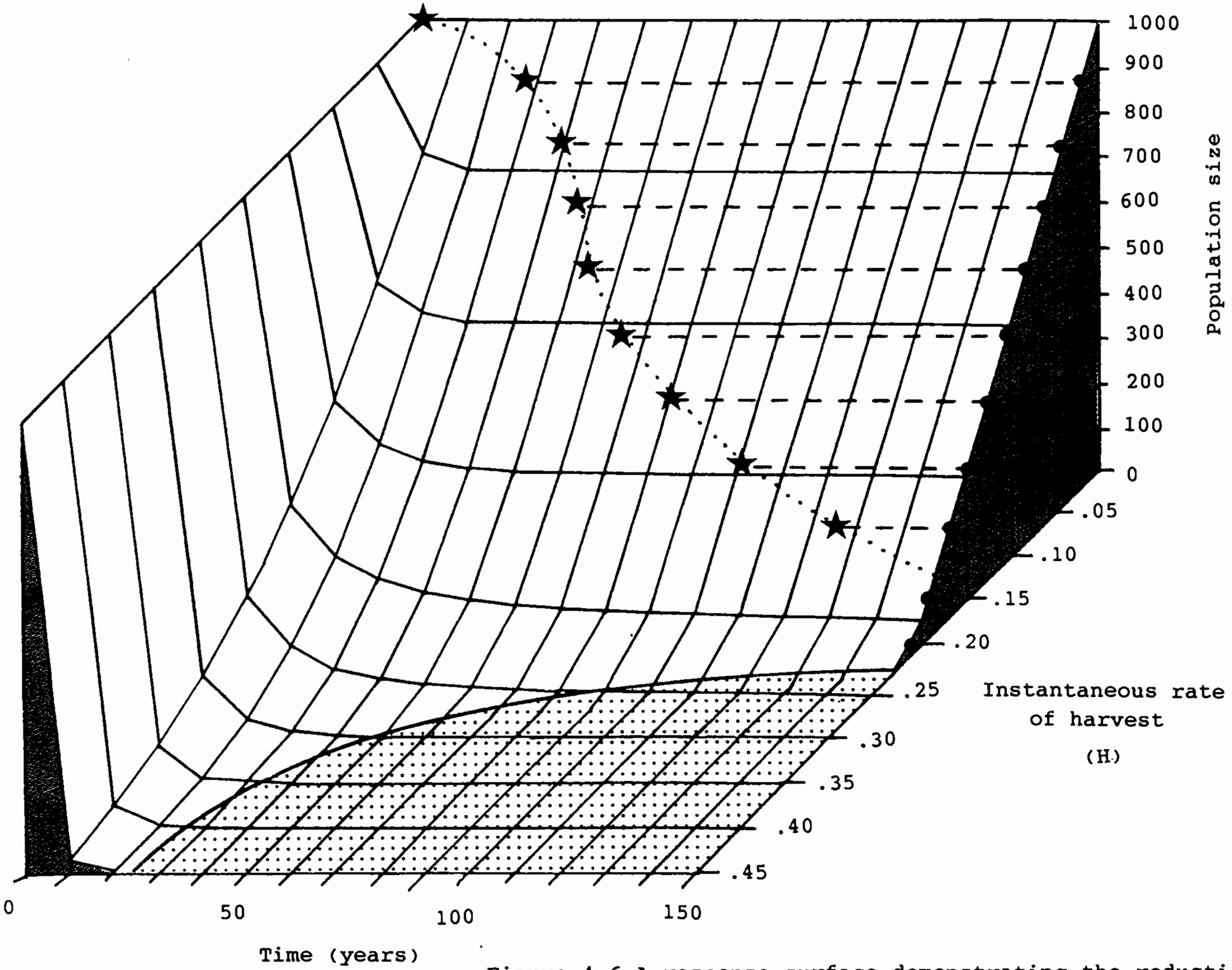

Figure 4.6 A response surface demonstrating the reduction in the size of a population of 1,000 donkeys achieved using 10 rates of instantaneous harvest (H) over 150 years. The stippled area indicates eradication of the population, while the dotted line indicates the time taken to stabilize the population under different harvesting rates (H). Stars on the line indicating population stability give the time taken to stabilize the population at 10 controlled population sizes (N_C), and the instantaneous rates of harvest (H) required to stabilize the population at N_C.

of animals removed. The cost of each removal is reassessed as population density falls and is summed to give the cost of the total cull for year y. These annual costs are then accumulated over the period of assessment Y, to give the cumulative cost of control for the proportional reduction achieved. If these cumulative costs of control are assessed for the population of 1,000 donkeys at 10 levels of N_c over 150 years, a response surface equivalent to that generated for instantaneous reduction in Figure 4.5 can be calculated for proportional reduction (Figure 4.7). Arrows indicate levels of N_c not attained within 150 years using a proportional reduction strategy.

To examine the relative costs of instantaneous and proportional reduction as strategies for control of feral donkey populations, the response surfaces generated to estimate the cumulative costs of controlling a population 1,000 donkeys were compared. The costs incurred by proportional reduction (strategy 2) were subtracted from those incurred by instantaneous reduction (strategy 1). Figure 4.8 illustrates the differences in cumulative costs associated with each strategy. Instantaneous reduction was always more expensive than was proportional reduction, with the difference most extreme when large scale reductions were considered over shorter periods of time. Again arrows indicate levels of N_c not attained using a proportional reduction strategy within the 150 years assessed.

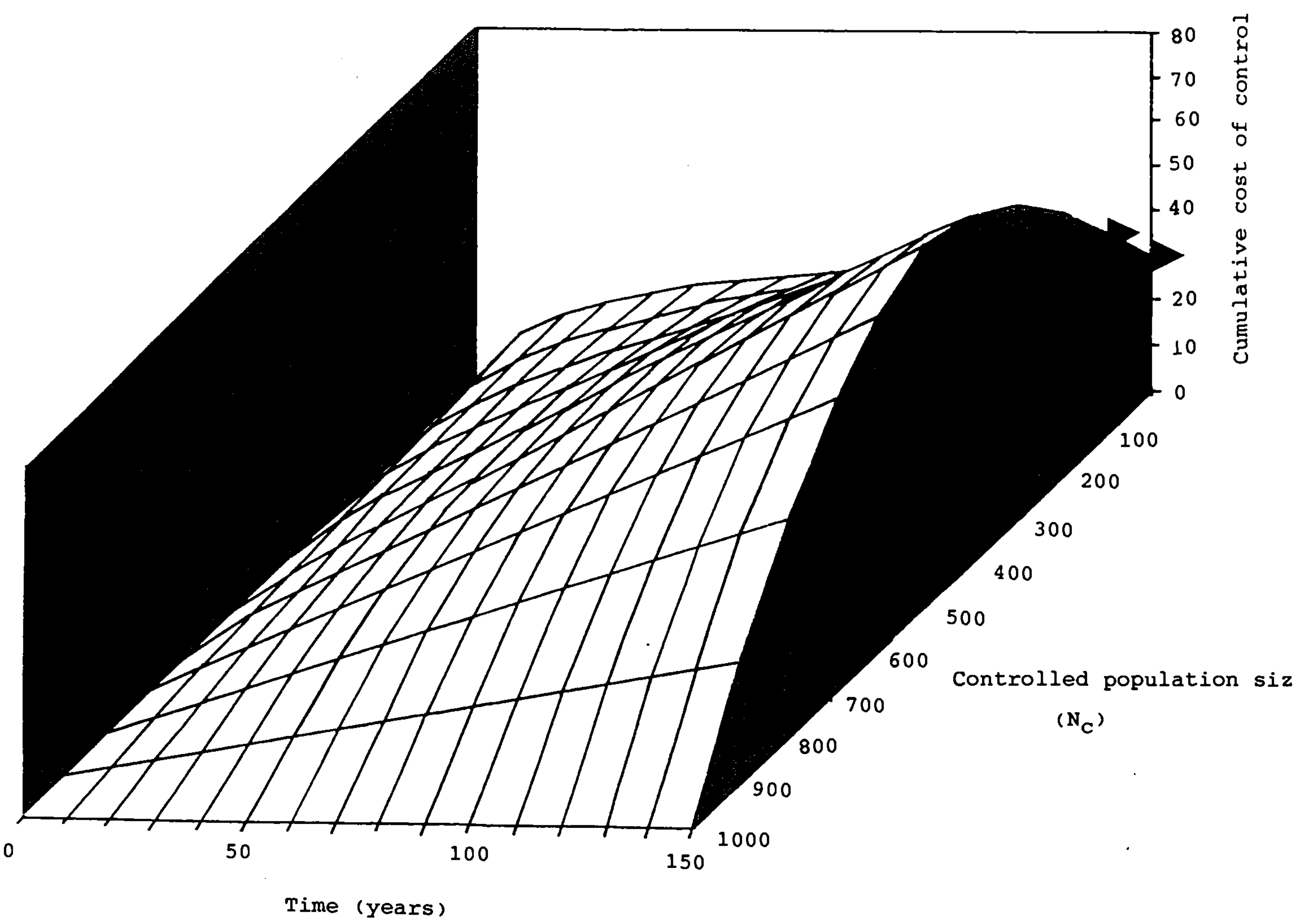

Figure 4.7 A response surface demonstrating variation in the cumulative cost of controlling a population of 1,000 donkeys at 10 controlled population sizes (N_C), over 150 years, using the proportional reduction strategy described in the text. Cumulative costs are the helicopter hours required to achieve and maintain the specified level of control. The arrows indicate that reduction to N_c is not achieved within the 150 years assessed in the Figure. The initial population of 1,000 donkeys is assumed to be at equilibrium density.

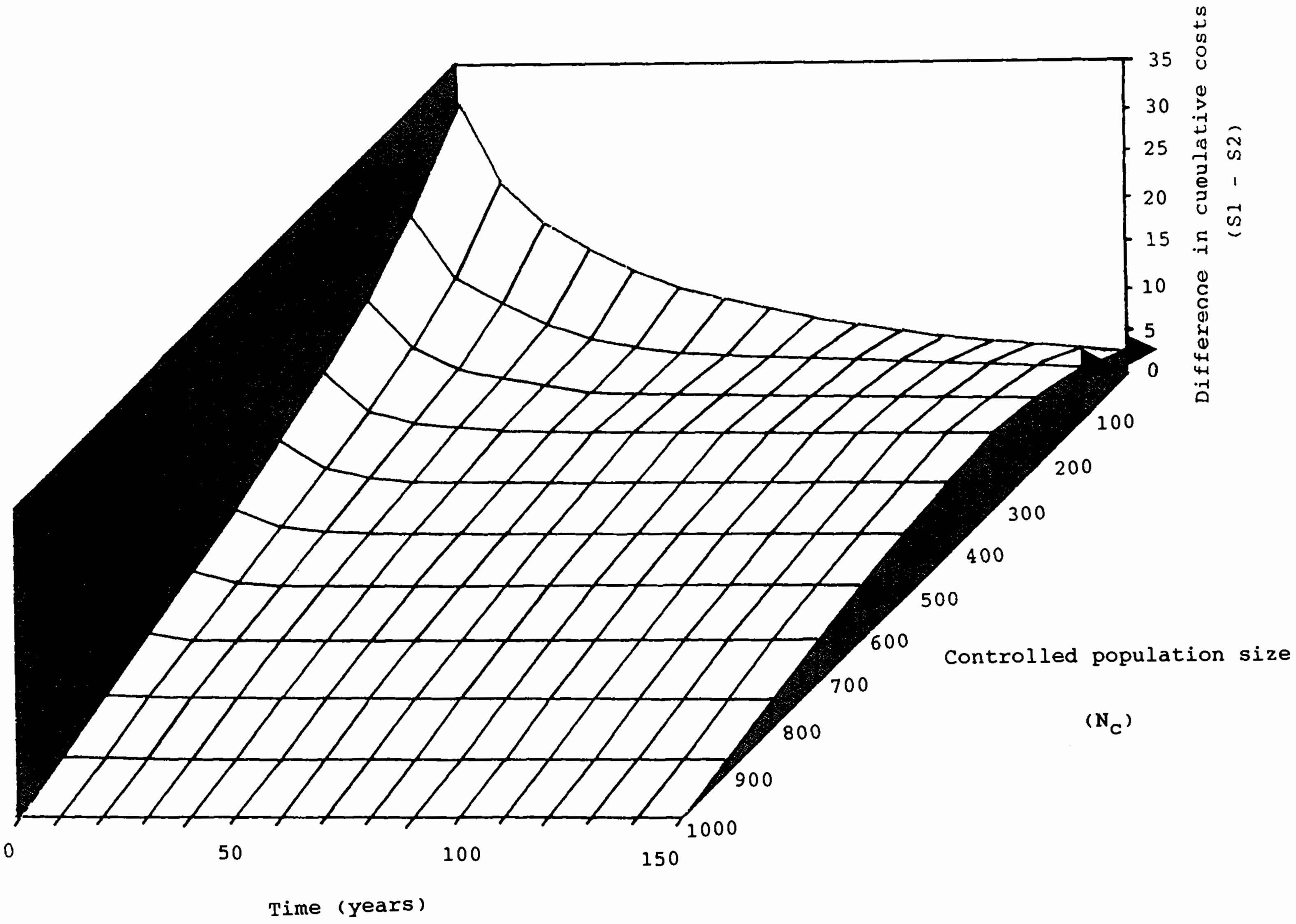

Figure 4.8 A response surface describing the difference in cumulative costs of controlling a population of 1,000 donkeys by instantaneous reduction (strategy 1), and proportional reduction (strategy 2). Arrows indicate levels of N_C proportional reduction does not achieve within the 150 years assessed in the Figure.

The two control strategies considered here represent two extremes of a continuum of potential strategies for donkey control. Intermediate to instantaneous or proportional reduction would be cases where reduction to N_C would be achieved over more than a year, but the instantaneous harvest rate imposed during this reduction process would be greater than that which would eventually stabilize the population at N_C ($H > H_S$). By increasing H above H_S, reduction to N_C is accelerated. After reduction to N_C is attained H could be reduced to a level sufficient to simply remove HN at N_C.

4.4 DISCUSSION:

Population productivity and the cost of donkey removal

The logistic model of population productivity used to model the cost of long-term donkey control in this study is probably not the most realistic productivity model that could be used for feral donkeys. A productivity model based on an interactive model of population regulation (Caughley 1976; Caughley & Lawton 1981), would be more appropriate than the logistic model used here. Models describing interactive systems of population regulation in herbivores have as a general property a peak in population productivity around 0.7(K) as opposed to the peak around 0.5(K) implied by the logistic model (Caughley 1976; Caughley & Lawton 1981). The effect of using an interactive model to predict population productivity from population density rather than the logistic model used here, would be to "flatten-out" the peak in C_{res} as prevailing population density increased (Figure 4.4b). This flattening-out would occur because HN would more closely reciprocate the exponential rise in the cost per donkey removal as donkey density decreases (Figure 4.3). This change in the relationship between C_{res} and population density would be reflected in a similar flattening of the peak in the cumulative cost of population control as N_c decreases (Figures 4.6 and 4.7). As such, the use of the logistic model in the current analysis may provide somewhat biased estimates of the costs of long-term feral donkey control. The logistic represents a necessary approximation for the purposes of this study, and is used in the absence of data neccessary to estimate parameters for the more realistic interactive model (Caughley 1976).

The removal of donkeys by shooting from helicopters appears both theoretically and empirically to be analagous to predators removing prey. The relationship between the time taken to remove each donkey from a population (here equated with the cost per donkey removed), and prevailing donkey density reflects the inverted functional response curve expected from predator-prey theory. Thus the Michaelis-Menten function predicts that the donkey density where saturation of the cost per donkey removed occurs will be at densities around 7 or 8 donkeys per km^2. At saturation densities, the cost per donkey removed approaches 0.01 hours of flight time, the equivalent of 80 to 90 donkeys removed per hour (Figure 4.3). Similar estimates of the rate of donkey removal at saturation densities have been independently derived for populations in northern Australia (APBWA 1986).

The cost of population control

The approach to assessment of the costs of long-term control of feral donkey populations adopted in this study can be used to project resource requirements for planned control work. Such projections can be used to assess the relative efficiencies of various strategies available for donkey control. Comparison of the two control strategies considered in this study demonstrates that proportional reduction is a consistently cheaper option than is instantaneous reduction (Figure 4.8). However, following attainment of N_C by either strategy, the number of donkeys that must be removed to restrain the population at N_C will be HN, and hence the cost of ongoing control beyond this point will be identical for the two strategies. Differences in cost between the two strategies lie in the way each achieves initial reduction of the population to N_C. Although proportional reduction is consistently cheaper it does not achieve population reduction to N_C for some years (dependent upon H_S) after the control program begins. In contrast, instantaneous reduction achieves population reduction to N_C in the first year of control.

Persistence of higher donkey densities over longer periods of time when proportional reduction is considered would presumably detract from any benefit/cost ratio indexing the efficiency of this particular strategy. Thus if assessment of instantaneous and proportional reduction considers potential benefits of control relative to the costs that such control would incur, rather than simply program costs alone; the two strategies may return similar measures of relative efficiency. The benefits derived from feral donkey control in northern Australia have yet to be examined.

It is emphasized that instantaneous and proportional reduction represent only the extremes of a suite of potential control strategies. Assessment of the costs involved in intermediate strategies would presumably return estimates of cumulative costs intermediate to those reported for the two strategies considered here.

The two components of the cost of control identified and estimated in this study (annual population productivity and the cost per pest removed), must be known in order to forecast the potential costs involved in ongoing pest control. In the case of donkeys in northern Australia, to use the models described here to examine benefit/cost relationships for ongoing control (eg: Tisdell 1982; Collins *et al.* 1984), the potential returns derived from donkey control must first be identified and measured.

GENERAL DISCUSSION OF RESULTS

The major objectives of this study related to the responses of feral donkey populations reduced below densities at or close to ecological carrying-capacity. The specific objectives were:

1. To examine the rate of increase generated by feral donkey populations in northern Australia that were at densities below ecological carrying-capacity.
2. To investigate factors that ultimately regulate the abundance of feral donkeys, and the demographic mechanisms through which these factors operate.
3. To examine the implications that the rate of recovery observed in feral donkey populations have for the cost of long-term population control.

Rate of population increase was derived independently from the examination of two recovering donkey populations. The two estimates were in close agreement, suggesting that the rate of increase in populations below carrying-capacity was around $r = 0.20$, or approximately 20 percent per annum. The effect of population density on growth, body condition and demography was examined to test an hypothesis that population abundance was regulated through density dependent mortality due to food shortage. Donkeys at high density grew more slowly and were in poorer body condition than were donkeys at low population density, suggesting that feral donkey population abundance was ultimately regulated by available food resources. The primary demographic mechanism through which food limited population size is mortality over the first six months of life. Thus at low population densities, the rate of juvenile mortality is relatively low and populations generate a positive rate of increase. As densities approaching ecological carrying-capacity are attained, food becomes harder to obtain and juvenile mortality increases accordingly. There is a corresponding decrease in the rate of population increase.

The observed rate of increase in recovering populations was incorporated into a numerical model derived to define a cost function for feral donkey population control. A density dependent population productivity function was combined with a function relating the cost per donkey removed to population density to predict the cost of reducing a population to, and restraining a population at some specified control density. The utility of the model was demonstrated by comparing the accumulated costs of control using two control strategies.

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