

## Live-trapping of the Northern Hairy-nosed Wombat (*Lasiorhinus krefftii*): Population-size Estimates and Effects on Individuals

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### Abstract

The northern hairy-nosed wombat, one of the most endangered large mammals known, occurs only in Epping Forest National Park, central Queensland. The results of a 3-stage trapping programme, carried out between 1985 and 1993, were used to estimate population size by means of three separate modelling approaches: minimum number alive (MNA), mark-recapture, and trapping effort. Trapping procedure varied among sessions, and each estimator was applied to sessions only where its use was appropriate. The population-size estimate for 1985-86 was 67 (trap effort) with MNA of 58; for 1988-89 it was 62 (Jolly-Seber mark-recapture estimate), with MNA of 48 and upper 95% confidence limit of 77; and for 1993 it was 65 (Chao mark-recapture and trap effort), with MNA of 43 and upper 95% confidence limit of 186 (Chao mark-recapture). No population trends were observed, although variability in estimates and wide confidence intervals meant that power to do so was limited.

Trapping affected the health and behaviour of wombats. Animals that were trapped twice within 10 nights lost an average of 0.62 kg ( $P = 0.006$ ) between captures. Wombats that were trapped twice within the first four nights of traps being set on a burrow showed less weight loss than those trapped for the second time after 5-7 nights (0.23 kg v. 1.54 kg). The effects of trapping appeared to remain with animals for some time, since animals trapped twice more than 30 nights apart and within six months weighed an average of 0.5 kg less ( $P = 0.013$ ) on second capture. When areas were trapped twice in succession with a 3-week gap, population-size estimates were lower for the second period of trapping. Thus, some wombats may have temporarily left areas disturbed by trapping.

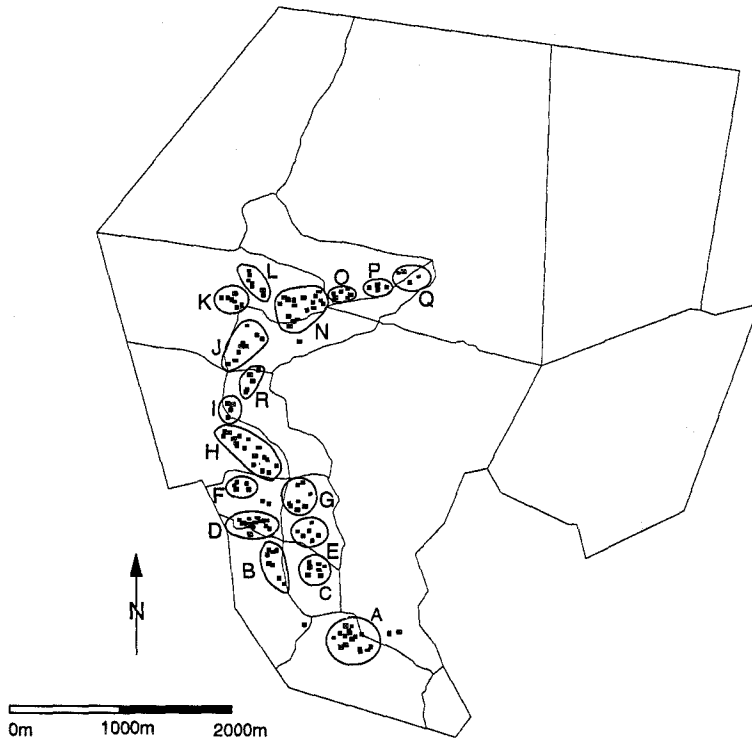
The deleterious impact of trapping may be reduced by restricting trapping to periods of four nights. Trapping effectiveness may be increased by minimising disturbance immediately before trapping and by moving traps between periods of trapping.

### Introduction

The northern hairy-nosed wombat [*Lasiorhinus krefftii* (Owen)] is one of the most endangered large mammals known. The sole remaining population has been estimated to number roughly 70 animals (Crossman *et al.* 1994) and occupies an area of only 300 ha in Epping Forest National Park, north-west of Clermont in central Queensland. *L. krefftii* was probably uncommon at the time of European settlement, and has been recorded from only three sites. Having disappeared from two of these, it has clearly declined, probably as a result of the effects of cattle grazing. Its range in the Epping Forest area has decreased in recent years (Crossman *et al.* 1994), apparently for similar reasons. The species is currently managed under a recovery plan funded by the Australian Nature Conservation Agency, and since 1985 has been the subject of an intensive trapping programme.

*Lasiorhinus krefftii* are herbivorous marsupials of the semi-arid plains of eastern Australia. Their remaining habitat comprises very deep sandy soils and vegetation ranging from grassland to open woodland (Steinbeck 1994). They are extremely shy and are seldom seen in the wild, as they spend the day in large burrows and feed nocturnally. *L. krefftii* are amongst the world's largest burrowing animals (Triggs 1988) and weigh up to 40 kg. Most burrows are spaced along the banks of a sandy gully and occur in groups, which usually consist of one or more large burrows with several entrances (up to seven), surrounded by a number of single- or double-entrance burrows (Fig. 1). Each wombat uses several burrows for daytime refuge, with about 50% of days in a 'home' burrow (Johnson 1991). Their diet consists mostly of native grasses (Crossman 1988).

In the management of any species, knowledge of the population size and information on population trends are usually considered to be of fundamental importance. Caughley (1994) has identified two competing paradigms in conservation biology. The 'small population paradigm' seeks to understand threats to a population that exist by virtue of the smallness of the population. These include demographic stochasticity, genetic drift and loss of heterozygosity. In assessing the risks posed by these threats to the population, an estimate of its actual size at a particular time is obviously necessary. The 'declining population paradigm' is concerned with identifying and ameliorating the processes that have caused a decline. Following this approach, knowledge of the actual size of the population at a particular time is less important than an estimate of the trend in the population through time. Relative indices, rather than absolute measures of population size, may therefore be adequate. Such an index, burrow activity, has been used to estimate changes in wombat population size. A problem with relative indices,



**Fig. 1.** Map of Epping Forest National Park, showing locations of burrows. Groups defined as systems for trapping effort population estimates are circled.

however, is the implicit assumption that the index is related to actual population size by a proportionality constant that does not change (Pollock 1995). This assumption cannot be tested without several estimates, through time, of the actual population size.

Actual population size and population trends may be necessary for quite different management purposes. Trends are probably the most important criteria for assessing the value of particular management interventions, such as habitat manipulation. In many cases, however, the most appropriate method of estimating trend is not population estimation through time, but by estimation of demographic parameters that can be used, by means of simple models, to extrapolate population trends (Taylor and Gerodette 1993). If management interventions that require removal of animals are contemplated (for example, removal for a 'last ditch' captive-breeding programme, or removal for a translocation), actual population size will be much more important.

In this study, a range of estimation methods are applied to trapping data obtained on the northern hairy-nosed wombat since 1985. The methods are compared as means of estimating both trends in the population and population size, and the results are compared with the trends suggested by burrow-activity monitoring. However, the behaviour of the wombats and the sampling design are such that the assumptions of every model used in population-size estimation may be to some extent violated. This problem is common to all investigations of real-world capture-recapture data. A variety of methods are employed, each requiring slightly different assumptions, affected in different ways by deviations from those assumptions, and none appropriate to all of the three sampling sessions. Deviations from assumptions are tested for where possible. In this way consensus estimates are sought and the capabilities of the various approaches are explored.

The study exemplifies many of the challenges associated with understanding the population ecology of an extremely rare species. Trapping inevitably involves stressing the animals, and it is essential to evaluate the quality and value of the data arising from a trapping programme against the costs to the species of the trapping programme itself.

The trapping programme was designed to provide data on the population structure, the incidence of breeding, social structure and body condition (Johnson 1991; Johnson and Crossman 1991; Crossman *et al.* 1994), in addition to determining the size of the wombat population.

## Methods

### Trapping

Data come from three major trapping exercises, or 'sessions'. The first was carried out between 1985 and 1987 and is summarised by Crossman (1988). The second was performed between late 1987 and mid 1989, and the third was carried out during 1993. The timing and locations of all captures during these sessions are shown in Fig. 2.

All three trapping sessions used similar methods, described by Crossman (1988). Tunnel traps were placed at burrow entrances, so that wombats could leave or enter burrows only through the traps. Untrapped entrances to multi-entrance burrows were fenced or otherwise blocked.

Newly trapped animals were sedated, and marked by a tattoo on one ear. Drawings were made of both ears and distinguishing marks noted. Tag loss was negligible. Retrapped animals were also usually sedated, processed and released into the capture burrow.

Trapping in a session did not proceed in a consistent way in all three sessions, as may be seen in Fig. 2. In Sessions 1 and 2, traps were not moved systematically between burrow systems, because trapping was aimed primarily at catching as many animals as possible rather than estimating population size. The third session, however, was subdivided into five separate intervals of trapping. Burrows were combined into five 'trap groups', and all active burrows in a trap group were trapped at the same time. During each of the five trapping intervals a trap group was trapped for a week or more, and then the traps were moved to the next trap group for another week. The traps were left there for the beginning of the following interval. Only one group was trapped in the first trapping interval. The final trap group was trapped during only one interval. Twice as many traps were used during the 1993 session as were used in earlier sessions, so that more entrances were trapped, fewer were blocked and trapping proceeded more quickly.

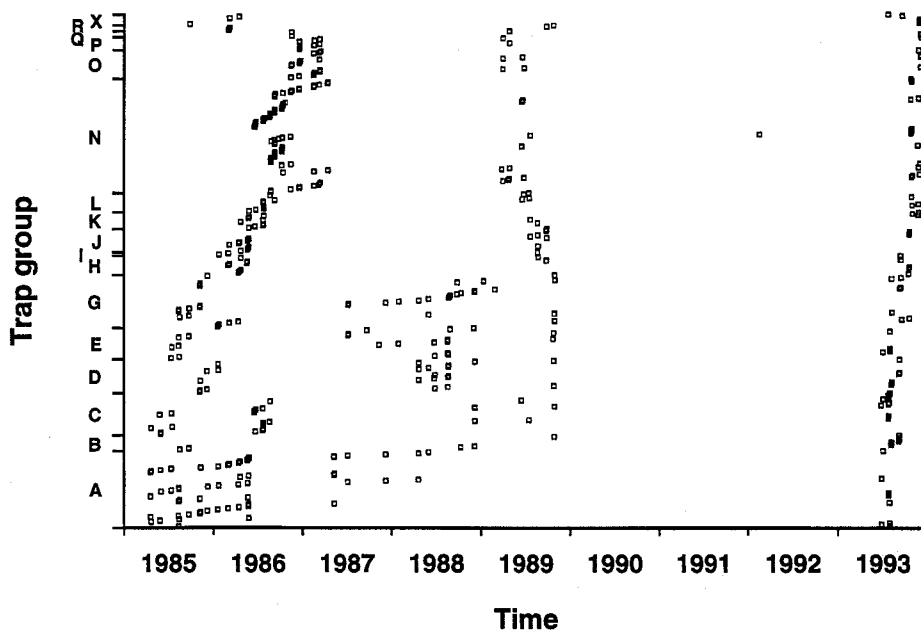


Fig. 2. Date of trapping against location for animal captures between 1985 and 1993. Location denotes the system in which the animal was captured. The first seven systems (A–G) are at the southern end of the park; the others are further north.

The traps were not always able to hold young animals, since animals below a certain size could burrow between the bars in the floor. On several occasions traps were found with mechanisms triggered and holes dug through the floor. Some small animals were captured when researchers reached the trap before the wombat could escape.

In all three sessions all active known burrows were trapped. Traps were left over burrows for long periods (four days or more in 83% of cases), so that wombats would have found it difficult not to emerge and feed.

However, some animals may not have been captured, for the following reasons: (i) some active burrows may have appeared inactive, and not been trapped; (ii) the activity of mending fences and setting traps may have caused wombats to leave an area before their burrow was trapped; (iii) animals may have avoided capture by staying down their burrows until traps were removed; and (iv) animals dug under fences and around traps, and some traps failed to go off when triggers failed, doors became stuck, or the animal stepped over the tripwire. Wombats that escaped in this way may have been trapped elsewhere on entering a burrow, or moved to untrapped burrows and avoided capture.

#### Analysis

The analysis methods may be divided into three broad approaches, all of which used data from the trapping programme carried out between 1985 and 1993. First, the minimum number known to be alive (MNA) was determined throughout the trapping programme. Second, mark–recapture modelling gave population-size estimates for the second and third trapping sessions, and survival rates between the first and second sessions. Third, trapping-effort models gave population estimates for the first and third sessions. Because of differences in the organisation of trapping sessions, some of the population-size estimation techniques could be used only on data from the final session (see Table 1).

Trap response and heterogeneity in capture probability through time and among individuals can influence the reliability of estimates and the choice of models in all three approaches. These factors were considered mainly for the third session, because more of the population-estimation methods were used on this session, and because data were more comprehensive.

**Table 1. Population-size estimates produced by each method for the three sessions**

Method		Session 1	Session 2	Session 3
Minimum number alive		*	*	*
Mark-recapture	Jolly-Seber	-	*	-
	CAPTURE modelling	-	-	*
	Order of capture	-	-	*
Trapping effort		*	-	*

*Trap response.* Capture probabilities on consecutive nights within a trapping period in the third session may not have been independent. Goodness-of-fit tests in programme CAPTURE (a program for mark-recapture population-size estimation: Rexstad and Burnham 1991) compared models that include trap response with models that do not to determine whether trap response was significant. These tests were performed for Periods 1 and 2 in the third session.

*Temporal heterogeneity in capture probability.* Temporal heterogeneity in capture probability during the third session may have occurred both among trap periods and among nights within a period. Mean capture-probability estimates from CAPTURE were compared for the first and second periods. Heterogeneity within Periods 1 and 2 was examined by comparing the number of animals captured per night with time since traps were set, and by means of the goodness-of-fit tests in the programme CAPTURE.

*Individual heterogeneity in capture probability.* All animals may not have the same probability of being caught. If animals are trap-happy or trap-shy, population-size estimators will be significantly biased (Otis *et al.* 1978). This kind of heterogeneity is very common in wild populations.

The distribution of individual catchability by trap period will differ from distribution by session, but both are likely to be heterogeneous, depending on the timidity of the animal and its ability to fast.

The goodness-of-fit tests from CAPTURE were used to test for individual heterogeneity in capture probability per trap period. Heterogeneity for the entire third trap session was searched for by fitting the Poisson distribution to frequency of individual trappings. Individual heterogeneity within other sessions was not observable because captures other than the first of each animal were not always recorded during those sessions.

#### *Minimum Number Alive (MNA)*

The minimum number of wombats known to be alive (Hilborn *et al.* 1976) was calculated monthly. A wombat was known to be alive at time  $x$  if it was trapped or otherwise identified both before and after  $x$ . It was also assumed to have been a member of the population for a time equal to its estimated age before its first capture. Animals more than 1.0 m in body length were considered to be adults, at least 2.5 years old (after Crossman *et al.* 1994). Animals less than 1.0 m long were assumed to be at least one year old.

#### *Mark-Recapture Estimates*

Several forms of mark-recapture estimation were used: Jolly-Seber analysis with programme JOLLY (Pollock *et al.* 1990), to estimate survival and recapture rates as well as population sizes; a method using the order and timing of captures during 1993 to estimate population size (Becker 1984; Niels Becker and Quanxi Shao, personal communications); and closed-population methods using programme CAPTURE (Rexstad and Burnham 1991).

#### *Jolly-Seber*

Open-population models allow estimation of population size in the presence of birth and immigration, death and emigration. Thus it was possible to use data from all trapping events between 1985 and 1993 in one statistical process.

For the Jolly-Seber analysis, data were pooled so that each of the three sessions was treated as a single trapping event. Estimates were made in two ways: first, all animals were included; and second, only

animals assumed to be adult (> 2.5 years old) were included. Survival rates probably vary between juveniles and adults, and therefore survival rates were calculated for adults alone. However, this kind of heterogeneity in survival rates has little effect on Jolly-Seber population-size estimates (Pollock 1981), so population sizes were calculated with all animals included.

Jolly-Seber methods allow the fitting of several different models to the data. The probability of capture can be assumed to either vary among sessions or remain constant. Similarly, survival between sessions can be assumed to either vary or remain constant. *A priori* observation implied variable models for both parameters. This was because trapping intensity varied among sessions, and because climatic conditions, which probably affect survival rates, were substantially different during the two intervals. However, adult survival rates may not be greatly affected by drought, so constant survival rate may be valid for the adults-only model.

In addition, models can assume trap response, with a different probability of capture for first and subsequent captures. However, trap response between sessions is unlikely given the number of years between sessions, and so the more parsimonious lack of trap response was assumed.

#### CAPTURE modelling

The computer programme CAPTURE calculates population size based on the changing proportion of previously captured animals caught in a series of consecutive trapping occasions (in this case, trap-nights). CAPTURE could be used only on the third trapping session (1993) because trapping was not structured appropriately in other sessions.

Most burrows were trapped during two separate periods of more than five nights, and population size was estimated for each period. The second period of trapping did not cover 18 of the 172 burrows (10.4%). Captures were labelled with the number of nights that traps had been set on the capture burrow during the period, and night of capture was used to represent trapping occasion. Otis *et al.* (1978) recommend that the number of trapping occasions be large (>5).

CAPTURE produces selection indices (a value between zero and one, where the best-fitting model is assigned the value one) for models including the null model ( $M_0$ ), trap response ( $M_p$ ), time heterogeneity ( $M_t$ ) and individual heterogeneity ( $M_h$ ), and combinations of the above (e.g.  $M_{th}$ ,  $M_{tbb}$ ) in capture probability. To do this it combines the results of a number of goodness-of-fit tests, including those outlined above. A selection index greater than 0.75 indicates a model appropriate for use with the dataset (Otis *et al.* 1978).

CAPTURE then produces estimates based on selected models. Two estimators are available for the  $M_h$  model: the Chao and the jackknife estimators, each of which is appropriate in different circumstances.

#### Order-of-capture Methods

A method developed by Becker (1984) employs the order of multiple captures in continuous time to estimate the size of a closed population. The method allows heterogeneous capture probabilities among animals. It relies on the generalisation that, as more of the population are captured, the number of animals caught multiple times will increase relative to those caught for the first time. This method could be applied only to the 1993 data, since retrapped animals were not always recorded during the earlier trapping sessions.

A general estimating equation for the estimated population size, is given by

$$C_1 - \frac{2}{k} \sum_{i=1}^k \int \frac{\hat{v} - C_1}{C_j - C_{j+1}} dC_{j+1} + \int \frac{\hat{v} - C_1}{C_{k+1} - C_{k+2}} dC_{k+2} = 0 \quad (1)$$

where  $k$  is a positive integer,  $C_k$  gives the number of animals caught at least  $k$  times, and  $dC_k$  is the change in  $C_k$  between successive captures.

The standard error in  $\hat{v}$  for any  $k$  is given by

$$\text{s.e.} = \frac{\left( C_1 + \frac{4}{k^2} \sum_{j=1}^k \int \left( \frac{\hat{v} - C_1}{C_j - C_{j+1}} \right)^2 dC_{j+1} + \int \left( \frac{\hat{v} - C_1}{C_{k+1} - C_{k+2}} \right)^2 dC_{k+2} \right)^{\frac{1}{2}}}{\frac{2}{k} \sum_{j=1}^k \int \frac{dC_{j+1}}{C_j - C_{j+1}} - \int \frac{dC_{k+2}}{C_{k+1} - C_{k+2}}} \quad (2)$$

(Niels Becker, Quanxi Shao, personal communication).

Appropriate values of  $k$  were chosen with a method based on Burnham and Overton's (1978) method for the jackknife. This involves selecting the lowest value of  $k$  where  $\hat{v}_{k+1}$  is not significantly different from  $\hat{v}_k$ . Estimates that were negative or had very high standard errors ( $>200$ ) were ignored.

Captures were ordered by the time since traps had been set on the capture burrow. Population sizes were calculated for both the first and second periods of trapping in 1993. The second period of trapping did not cover 18 of the 172 burrows (10.4%).

#### *Trapping Effort*

The population size was estimated on the basis of trapping effort, following a method used by Crossman *et al.* (1994). This method estimates population size as the asymptote of a plot of cumulative individuals caught against effort. The method assumes that trap success does not change with time.

#### *Effect of Trapping on Wombats*

Trapping may have affected the health and behaviour of the wombats. Traps were left on burrows for long periods and untrapped entrances were blocked, so that some animals may have fasted for over 10 nights to avoid traps. The effects of trapping were observed by examining the weight change of animals caught more than once. Weight changes were grouped by number of nights between captures and number of nights underground before second capture.

Data used in this analysis are not comprehensive, because the date when a trap was set was not recorded for all trapping events. In addition, many animals trapped for the second time in a short period were released without being weighed. However, the data available were considered to be a representative sample.

Trapping may also have disturbed the wombats enough to cause them to leave the trapped area as soon as they were able, and to move to untrapped burrows. To look for evidence of this, CAPTURE population-size estimates were compared during Periods 1 and 2 of Session 3.

## **Results**

### *Trap Response*

CAPTURE's goodness-of-fit tests, applied to Session 3, did not indicate significant trap response in either the first ( $M_0$  v.  $M_b$ ,  $\chi^2 = 0.380$ , d.f. = 1,  $P = 0.537$ ;  $M_h$  v.  $M_{bh}$ ,  $\chi^2 = 2.00$ , d.f. = 5,  $P = 0.849$ ) or second period ( $M_0$  v.  $M_b$ ,  $\chi^2 = 0.005$ , d.f. = 1,  $P = 0.942$ ;  $M_h$  v.  $M_{bh}$ ,  $\chi^2 = 0.429$ , d.f. = 5,  $P = 0.995$ ). However, the power of the tests was poor because of lack of data and the test's inherently low sensitivity.

### *Temporal Heterogeneity in Capture Probability*

Apart from the first night of the first trapping period of Session 3, when only one animal was captured, the rate of capture did not appear to change through time during a period (Period 1 without Night 1: mean = 5.83 animals per night, s.d. = 1.60,  $n = 6$  nights, range = 3–8). Disturbance while establishing the traps before Period 1 may account for the low probability of capture on the first night of this period. This trap-night was omitted from CAPTURE population-size estimation.

The mean probability of individual capture appeared to increase between Periods 1 and 2. Capture probability during the first period was estimated to be 0.10 ( $M_h$  jackknife estimate: Otis *et al.* 1978) and 0.09 ( $M_h$  Chao estimate: Chao 1989). Estimates for Period 2 were 0.22 for both methods. In other words, each individual had about a 10% chance of being caught per night during Period 1, and a 20% chance during Period 2.

Three factors may have contributed to this difference. First, the process of establishing a trap group before the first of the two trap periods may have lowered average trappability throughout the period. The next period began with quietly unlocking the doors and setting the traps, possibly resulting in higher capture probabilities. Second, animals may have become accustomed to traps by the time of the second trapping period. Third, trap-shy animals may have left the trapped area between the first and second periods.

### *Individual Heterogeneity in Capture Probability*

One wombat was captured 41 times during the study, on five occasions was captured twice in one night, and on one occasion three times. The median trappings per wombat over the study was three (upper and lower quartiles eight and two). At the other extreme, some wombats may have avoided capture altogether by remaining in their burrows until the traps were removed. This avoidance is impossible to quantify, but is illustrated by the fact that two animals that appeared not to have fed recently (abdomens noticeably less rounded than normal) were captured 12 nights after traps were first set on their burrows. On most other burrow systems, traps were removed or reset before this time. In the first session, burrows were trapped for an average of 5.5 consecutive nights, in the second for 5.3 nights, and in the third for 8.2 nights.

During 1989 an unsuccessful attempt was made to capture all the animals in a burrow system, by attaching radiocollars to captured wombats and targeting burrows known to be occupied (from distinctive sounds of wombat movement) by uncollared wombats. However, this attempt was not successful: eight animals were captured, but probably two or three remained uncaught. This suggests that some wombats were almost untrappable.

In addition, trapping effort varied among burrows, which would have influenced the likelihood of trapping individuals. Some burrow areas were trapped more intensively than others during the first two trapping sessions, and trapping effort was distributed differently among sessions.

CAPTURE's selection indices indicated that the heterogeneity model  $M_h$  was acceptable. During Period 1 the selection index for model  $M_h$  was 0.99, and 0.84 during Period 2 (recommended lower limit is 0.75) against 1.00 for the null model ( $M_0$ ) in both cases. However, individual variation in capture probability was not clearly demonstrated either during the third session as a whole ( $H_0$  = no variation,  $\chi^2 = 2.013$ , d.f. = 2,  $P = 0.366$ ) or in periods within it (first period,  $\chi^2 = 3.531$ , d.f. = 1,  $P = 0.0602$ ; second period,  $\chi^2 = 0.595$ , d.f. = 1,  $P = 0.441$ ).

### *Minimum Number Alive (MNA)*

In all, 53 animals were captured during the first trapping session, 45 during the second, and 43 during the third. The MNA was greatest in November 1985, when at least 58 animals were alive. MNA is followed through time in Fig. 3.

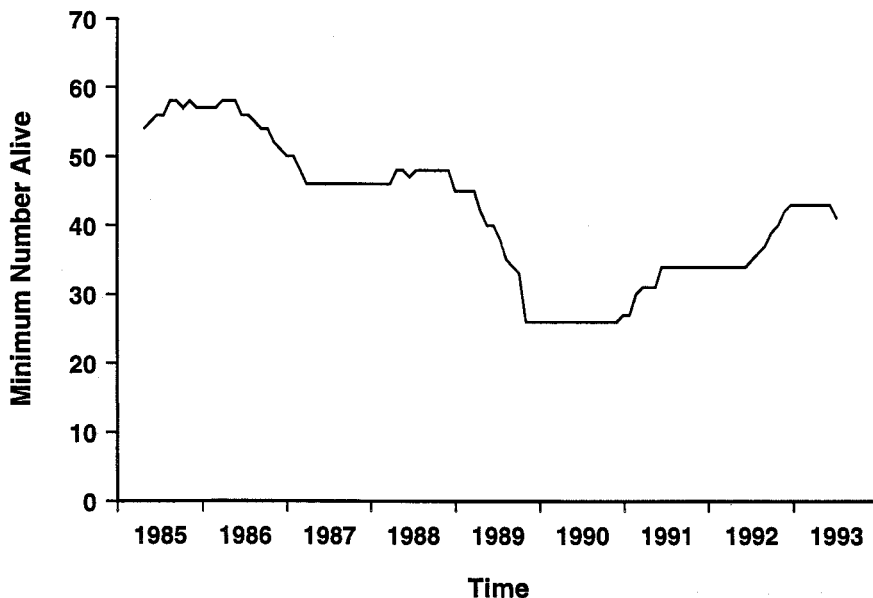


Fig. 3. Minimum number alive in the Epping Forest population against time.



*Jolly-Seber*

Jolly-Seber estimates of population sizes, survival rates and recruitment rates are provided in Table 2. Goodness-of-fit tests did not allow distinction between the constant-survival and the variable-survival models.

**Table 2.** Jolly-Seber estimates of population size, annual survival, capture rate and recruitment for Sessions 1-3

Group	Model	Variable	Period	Estimate	95% Confidence interval
All animals	Survival, capture rates vary with time	Population size	2	61.7	46.9-76.5
		Annual survival	1, 2	0.940	0.861-1.019
Adults only	Survival, capture rates vary with time	Population size	2	46.1	34.9-57.3
		Annual survival	1, 2	0.949	0.868-1.030
	Survival constant, capture rate varies	Population size	2	47.0	37.2-56.9
		Annual survival	3	55.6	24.8-79.2
		Annual survival	1, 3	0.951	0.870-1.032

*Closed-population Modelling*

CAPTURE modelling provided population estimates for Periods 1 and 2 of the third session. As detailed above, CAPTURE's model-selection procedures showed both the null and  $M_h$  models to be suitable for Period 1, but model  $M_h$  was considered more appropriate because of evidence from the field. Population-size estimates are shown in Table 3. The Chao estimator generally performs better than the jackknife for sparse data, provided at least five samples are taken (Chao 1988). The jackknife estimator usually underestimates population size when data are sparse (White *et al.* 1982), and the coverage of its confidence interval may also be poor in this situation. In this case the data are sparse since most animals (16 of 22) were caught only once, and six samples were taken. Thus the Chao estimate of 65 animals seems the most appropriate of all for the 1993 population.

Order-of-capture methods produced population-size estimates for Periods 1 and 2, which are given in Table 3. However, upper confidence limits for both periods were below the MNA for Session 3.

**Table 3.** Estimates of population size for the third session from the programme CAPTURE, the order-of-capture method and trapping effort

Method	Period	Population size	95% Confidence interval	Daily probability of capture
CAPTURE $M_h$ (jackknife)	1	55.0	39-85	0.103
	2	22.0	18-34	0.220
CAPTURE $M_h$ (Chao)	1	65.0	33-186	0.087
	2	22.0	17-42	0.220
Order of capture	1	31.5	22.5-40.5	-
	2	22.5	7.8-37.2	-
Trapping effort	Both	64.8	- <sup>A</sup>	0.660 <sup>B</sup>

<sup>A</sup>Not applicable.

<sup>B</sup>Value for the session.

### Trapping Effort

A trapping effort model showed that, between 1985 and 1987, 40 nights of trapping were enough to trap over 95% of the animals caught after 80 nights of trapping. Assuming that those areas trapped for fewer than 40 nights were not yet trapped out, population size in 1986 was estimated as 67 (Crossman *et al.* 1994).

A trap-success curve for the 1993 trapping session was not obtainable because few burrows were trapped for more than 20 nights. However, during the first 20 nights the trap-success curve followed the trajectory of the 1987 curve very closely, and this curve was used to predict trap success in 1993. The curve implied a capture probability ( $P$ ) of 0.79 for Session 1, and 0.66 for Session 3, and a 1993 population size of 65 animals (Table 3). This method could not be used to estimate capture probability or population size for Session 2.

### Effect of Trapping on Wombats

Wombats caught and weighed twice or more within 10 nights averaged 0.62 kg lighter on the later captures. The loss was associated with fasting, since average time since traps were set on the capture burrows was longer before second captures than before first captures (Table 4).

Weight changes of animals caught twice or more within 10 nights were further restricted by the number of nights that traps had been set on recapture. The loss observed among animals recaptured 5–7 nights after traps were set was higher (by 1.3 kg,  $P = 0.0033$ ) than for those caught twice during the first four nights (Table 5). Weight loss among animals recaptured after seven days of trapping was small, and statistically not significant. In all, 63% of captures (235 of 373) were made in the first four nights after setting traps, from 59% of the trap-nights (2613 of 4415).

Wombats caught and weighed twice within six months, with at least 30 nights between captures, were lighter at recapture by 0.5 kg (see Table 4). The loss was not seasonal, since

**Table 4.** Weight change between captures, and the number of nights that traps had been set on the burrow when the animal was captured, grouped by the number of nights between captures

Nights between captures	Weight change (kg)				Capture	No. of nights traps set			
	Mean	s.d.	$n$	$P^A$		Mean	s.d.	$n$	$P^B$
0–10	-0.62	0.97	23	0.0060	1st	3.32	2.40	22	< 0.0001
					2nd	6.09	2.47		
30–186	-0.50	1.76	81	0.0128	1st	3.55	1.93	69	0.4304
					2nd	3.42	2.08		
> 186	2.64	5.84	77	0.0002	1st	3.74	2.32	54	0.1218
					2nd	3.98	2.48		

<sup>A</sup>Probability that weight change equals zero (2-tailed).

<sup>B</sup>Two-tailed probability.

**Table 5.** Weight loss for animals caught twice or more within 10 nights, grouped by the number of nights that traps had been set on recapture

No. of nights traps set	Mean weight change (kg)	s.d.	$n$	$P^A$	Mean night of first capture	Mean No. of nights between captures	s.d.	Weight change per night (kg)
1–4	-0.233	0.273	6	0.045	1.33	1.83	1.17	-0.199
5–7	-1.538	1.088	8	0.003	2.38	3.63	2.20	-0.424
>7	-0.038	0.487	8	0.417	5.75	2.75	2.25	-0.017

<sup>A</sup>Probability that weight change equals zero (1-tailed).



Fig. 4. Mean weight of wombat on capture against nights since trap was set on capture burrow. Error bars are standard errors.

there was no difference ( $P = 0.318$ ) between mean month of first (mean = 7.05, s.d. = 3.45,  $n = 81$ ) and second capture (mean = 6.64, s.d. = 3.64,  $n = 81$ ). The loss was also not determined by increasing trap-shyness, since the number of nights since traps were set on the capture burrows did not change.

Consecutive captures more than six months apart showed a mean weight gain of 2.6 kg. The average weight of wombats captured increased during the first six nights of trapping on each burrow ( $P = 0.008$ ) (Fig. 4). However, the average weight of wombats captured more than six nights after traps were set on a burrow (mean = 25.63 kg, s.d. = 5.38,  $n = 34$ ) was less ( $P = 0.011$ ) than for wombats captured during the first six nights (mean = 28.16 kg, s.d. = 6.58,  $n = 208$ ). There was no significant difference in time of capture ( $P = 0.09$ ) between animals caught during the first six nights (mean = 0222 hours, s.d. = 3 h 46 min,  $n = 207$ ) and animals caught later (mean = 0145 hours, s.d. = 3 h 48 min,  $n = 34$ ).

Population-size estimates for Period 2 were lower than for Period 1 of the third session (Table 3), for both the CAPTURE and the order-of-capture methods. This result suggests that animals left the trapped area during Period 1 or during the break between the two periods.

## Discussion

Clearly, trapping has provided poor information on population trends. For this purpose it is unsatisfactory to have to use different estimators for different sessions. The apparent stability in population size is compromised both by the differences in estimation techniques and by the wide confidence intervals. The estimates suggest that wombat population size in 1985–86 was over 58 (MNA) and probably about 67 (trap effort), in 1988–89 was between 48 (MNA) and 77 (Jolly–Seber), and probably over 62 (Jolly–Seber), and in 1993 was between 43 (MNA) and 186 with an expected value of 65 (Chao and trap effort). It may be tentatively inferred that the population has not declined greatly between the second and third trapping sessions. It is possible that the population increased during this period, given the increase in upper confidence limit.

However, these estimates are more useful than those derived from burrow activity, a low-impact method for estimating wombat population trends. The average burrow-activity index increased between the first and second trapping sessions from about 45 to approximately 75 active burrows (Crossman *et al.* 1994). This 67% increase is much greater than the largest possible increase in population size in the same interval, from 58 to 77 animals (33%). Summer rainfall was consistently low during this period. It appears that the increased burrow-activity may have been mainly due to the increase in wombats' foraging range as habitat conditions worsened, as was suggested by Crossman *et al.* (1994).

There are also problems with these estimates as indications of absolute population size. One of the most important factors affecting population-size estimates is heterogeneity in capture probability (Otis *et al.* 1978), and circumstantial evidence suggests that it affects these results. Statistical tests were inconclusive, but their power was low. Evidence for both trap affinity and trap avoidance seems strong enough to assume that unequal catchability was always a factor. As Pollock and Otto (1983) point out, 'no estimator can account for extreme heterogeneity where animals have capture probabilities close to zero. If the population has a lot of these animals, all methods will have a severe negative bias'.

Among the population estimates, MNA provided a useful baseline. However, these estimates cannot uncover downward trends in the population size. A drop in MNA on the last capture occasion is a result of the way the estimate is calculated, and does not imply an actual reduction in population size (Pollock *et al.* 1990). The MNA for the second session was similar to that of the last session in that it excluded new adults caught during the last session. With more than 2.5 years between the two sessions, adults caught during the third session need not have been alive during the second. The drop in MNA between Sessions 1 and 2 may therefore not reflect a real drop in population size.

Jolly-Seber models provided a population-size estimate for the second trapping session, as well as useful estimates of survival rate. The wombat-trapping programme violated the assumption that sampling time is negligible compared with intervals between samples, since the first session lasted about 16 months, the second between six months and two years depending on the area, and the third five months. However, given the very high survival rates of adult wombats, the violation is unlikely to have affected the estimate. The assumption of no capture heterogeneity among individuals was also violated, which would have affected population-size estimates more than it did survival rates (Pollock 1981). However, population-size estimates are most robust to unequal catchability when probability of capture is high (Carothers 1973; Nichols and Pollock 1983), as in this case. Attempts to trap burrows out mean that this heterogeneity was probably lower over a full session than in shorter periods, but was probably still a factor. It is therefore likely that during the second session the population held more than 62 individuals, and that the upper 95% confidence limit of 77 is also too low.

The Jolly-Seber estimates for adults alone suggest an interesting increase in adult population size from Period 2 to Period 3, although the wide confidence intervals mean that the trend is not significant. The prevailing drought may have reduced the number of juveniles in the later period, resulting in little overall increase in population size.

For management purposes it is most useful to know population size during the most recent episode. However, Jolly-Seber methods provide no such estimate and MNA methods provide a flawed one. The methods that require a closed population are more likely to provide useful information, but their estimates vary in reliability, can have very wide confidence intervals and require specific sampling designs.

CAPTURE's population-size estimates for the first trapping period of 1993, 55 (jackknife) and 65 (Chao), were consistent with other estimates and greater than the MNA. As detailed in the results, the Chao value of 65 animals seems most appropriate for the 1993 population. However, the wide 95% confidence interval [43 (MNA) to 186] limits the usefulness of the estimate.

The order-of-capture method's estimates were all lower than the MNA, and in fact failed to include the MNA within the 95% confidence interval. These results therefore cannot be used to estimate overall population size. Order-of-capture methods can lose efficiency when capture probabilities are high (Wilson 1992), which may have contributed to the failure in this case.

Finally, trapping effort provides an estimate that is difficult to interpret, because of problems with the methodology and lack of standard errors. After allowing for the proportion of animals caught in more than one area, the trapping-effort method estimated the 1987 population to be 67 animals (Crossman *et al.* 1994). This technique is, however, problematic because of the possibility of either positive or negative bias. The reduction of new captures at the end of the session is due to reduced trapping-effort as well as to the trapping out of the population, so the result is negatively biased. A positive bias would have occurred because traps were removed first from trapped-out burrows, while burrows known to be used by untrapped animals were sometimes trapped for longer.

The assumption that the response of animals to trapping effort was the same in the first and third sessions introduced additional error, because trapping methods differed between sessions. More traps were used during the later session, so that more burrows were trapped at once and fewer entrances blocked. In addition, trapping periods were longer and more uniform in length. These factors could have changed the distribution of animals trapped per burrow night. Although the distributions for the two sessions appeared to parallel each other during the first 20 nights, variations after this time could have a large impact on the estimate of 64.8 animals.

#### *Can Trapping be Justified?*

There is a trade-off to be considered in obtaining information on declining wombat populations by trapping. Trapping has provided a useful picture of population composition and breeding rates, since each of the three sessions captured most of the population (Session 1, 79% of estimated population; Session 2, 73%; Session 3, 66%). However, trapping is expensive and time-consuming to carry out, the results have low power to uncover trends in population-size, and population size estimates are inaccurate. Perhaps the most serious drawback of all is its effect on the animals.

Trapping affects the health and behaviour of the study population. Wombats caught and weighed twice within 10 nights lost weight, presumably because they went without food to avoid traps. Weight loss appeared to occur in animals held underground for any period, although weight loss was less with less time underground.

Heavier wombats appeared to remain underground for longer, since during the first six nights of trapping the average weight of all wombats trapped increased with time. This implies that older animals are more cautious, or that larger animals are able to fast for longer periods.

However, after six nights the average weight of wombats captured dropped: those captured after traps had been set for more than six nights weighed on average significantly less than those captured sooner. Conversely, animals trapped twice within 10 nights, but captured for the second time more than seven nights after traps were first set, showed no significant weight loss between captures. There are several possible reasons for this. First, many of animals captured after the first week of trapping on a burrow may have managed to feed between captures, rather than emerging for the first time after a period underground. However, if these post-feeding animals were trapped on entry to a burrow, one might expect the average time of recapture to be later in the night. There was in fact no significant difference in time of capture between the two groups. Second, many of the animals trapped for the second time after seven nights may already have lost most of their gut weight (through digestion and defecation) by first capture, which occurred after 5.75 nights of trapping on average.

Animals caught twice within six months, with at least 30 nights between captures, also lost weight on average. This implies that trapping has long-term effects on the animals, apart from the short-term loss of gut weight. Wombats caught twice six months or more apart tended to gain weight, a change mainly due to the growth of juveniles.

Trapping also disrupts the behavioural patterns of the wombats, since they may change their movement patterns to avoid capture. Both CAPTURE and the order-of-capture methods estimated a larger population size for the first trapping period in 1993 than for the second period, even allowing for the slightly smaller sample in the second period. This is consistent with the hypothesis that animals moved out of trapped areas during the break in trapping. The CAPTURE method also estimated that capture probabilities were over twice as high during the second period. Thus, the trap-shy animals may have left, whilst those with high capture probabilities remained. The difference in levels of disturbance and trap familiarisation may also have had an effect.

Trapping has been the most accurate method available for estimating wombat population size. However, techniques are now being developed that are less disruptive, more reliable and accurate, quicker, and cheaper than trapping. DNA fingerprinting techniques can now identify individual wombats (Taylor *et al.* 1994) from single hairs (A. C. Taylor, personal communication), which are obtained by placing adhesive tape at burrow entrances. It would therefore be possible to estimate population size by hair-sampling burrows with a mark-recapture closed-population experimental design and the program CAPTURE. Combining this with the existing trapping data would allow long-term estimation of survival rates with Jolly-Seber open-population modelling.

However, some trapping may be necessary for other purposes, and this study indicates ways to reduce its negative effects. Wombats caught twice within four nights lost considerably less weight than those caught later. If traps are removed after four nights animals may be less affected, although this would increase the amount of trap-moving per wombat capture, and could reduce the chances of capturing some trap-shy wombats.

Setting traps for such short periods would make it important to minimise disturbance while setting up, which reduces trap success early in the period. If fences and other trap infrastructure are established or repaired long enough before trapping begins, animals driven away by disturbance may have time to return, particularly if there is disturbance elsewhere. Traps should also be moved after each period of trapping, because the disturbance associated with the first trapping period reduces the number of new animals caught in the following period.

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