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Long-term population trend of the common brushtail possum *Trichosurus vulpecula* in the Orongorongo Valley, New Zealand

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CHAPTER THIRTY-NINE

Long-term population trend of the common brushtail possum *Trichosurus vulpecula* in the Orongorongo Valley, New Zealand

M. G. EFFORD[1] and P. E. COWAN[2]

We analysed variation in the local abundance of the introduced Australian brushtail possum *Trichosurus vulpecula* over 35 years in native forest in the Orongorongo Valley near Wellington, New Zealand. Possums had occupied the mixed lowland forest for about 60 years at the start of the study, and continued to modify its composition by selective browsing. The population was studied by mark-recapture. The hypothesis tested was that vegetation changes were causing possum carrying capacity to decline. Mean annual population density was found to vary within a relatively narrow band (6.5–13.7/ha; mean 9.76 ± 0.26 SE). Density declined in the early years of the study (1967–1978) and later increased (1979–2001), but overall the linear population trend was slightly positive (+0.04 ± 0.025/ha/year) and markedly positive over the last 23 years (+0.16 ± 0.050/ha/year). Mean annual body weight of adult males (2 306 ± 17 g) exceeded that of adult females (2 199 ± 21 g) and showed a slightly negative linear trend over time for each sex (females: -3.4 ± 1.8 g/year, $P = 0.07$; males: -3.0 ± 2.0 g/year, $P = 0.06$). There was no overall change in possum biomass density over the 35 years of the study.

The change in population trend coincided approximately with unusually high mortality in 1977 and increased trapping effort on an extended grid from 1980. However, it was not possible to explain the population change as a methodological artefact, and we conclude that the upward trend of density over 1980–2001 was due to a gradual increase in carrying capacity. This is contrary to previous predictions that carrying capacity would decline because of the progressive elimination of preferred food species, but consistent with some other dynamic interpretations of the interaction between the possum and New Zealand forests. We suggest that palatable opportunist plant species may increase in the face of browsing by possums if they are sufficiently fast growing and resilient, with the result that possum carrying capacity is buffered against the loss of less resilient palatable species. Our results show that native forests modified by long-term herbivory can continue to sustain high possum densities that are a threat to secondary prey of conservation importance.

INTRODUCTION

COMMON brushtail possums *Trichosurus vulpecula* from Australia were liberated repeatedly throughout New Zealand in the nineteenth and early twentieth centuries to establish a fur industry. They have since become major economic and conservation pests, reaching high density in some native forests (Pracy 1962; Cowan 1990a; Efford 2000). Selective browsing by possums is believed to have systematically changed the floristic composition of some of these forests (Kean and Pracy 1953; Fitzgerald 1976, 1978; Meads 1976; Batcheler 1983; Payton 1985; Campbell 1990). Possums also prey on endangered native birds and invertebrates (Sadleir 2000). Rational management of native forests requires the prediction of possum population trends and an understanding of their interaction with the vegetation and other fauna. A common assumption has been that the sequential elimination of palatable species from New Zealand forests by possums would drive a long-term downwards trend in possum abundance. We call this the hypothesis of declining carrying capacity.

Long-term monitoring studies provide a test of this hypothesis. At Pararaki in the Haurangi Range, southern North Island, there was a large initial decline in possum numbers between 1946 and 1965, but subsequent annual sampling showed no trend over 1965–1976, a sudden decline in 1977, and an upward trend from 1977 to 1989 (Thomas *et al.* 1993). They interpreted the post-1965 pattern as ". . . irregular fluctuations around

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a more-or-less stable equilibrium abundance". Interpretation of these results is limited by their large sampling variance, the uncertain relationship between trap success and density, the unknown effect of annual removal trapping on the population, and the lack of ancillary information on diet and vegetation.

Our data are from a sustained mark-recapture study in native forest of the Orongorongo Valley near Wellington, New Zealand, from 1966 to 2002 (Crawley 1973; Fitzgerald 1976, 1978; Bell 1981; Ward 1978, 1984, 1985; Efford 1998, 2000). Possum browsing has caused substantial vegetation change at this site. Tree species with highly palatable foliage such as *Fuchsia excorticata, Alectryon excelsum,* and *Pseudopanax arboreus* were browsed heavily in the 1940s (Mason 1958) and these species later virtually disappeared from the area (Campbell 1984). Other palatable species (*Metrosideros robusta, Weinmannia racemosa*) continued to be browsed (Fitzgerald 1976; Meads 1976; Allen *et al.* 1997) and declined in abundance during this study (Campbell 1990). Bell (1981) specifically predicted that ". . . the carrying capacity of the Orongorongo forest will probably decline further as more food resources are depleted through selective browsing by possums and other herbivores". Subsets of the present data have been analysed previously and attention has been drawn to the relative constancy of possum numbers over time (Efford 1991, 1998, 2000; Brockie 1992; Nugent *et al.* 2001). Here we examine a longer time series more closely for evidence of a systematic trend in abundance.

A further motivation for describing the long-term dynamics of possum populations is to facilitate the analysis of shorter-term phenomena involved in population regulation. The time-series methods available for such analysis generally assume stationarity (constancy of parameters). Longer-term trend in parameters such as carrying capacity needs to be removed before time series analysis (e.g., Chatfield 1984; Berryman 1994). We intend to consider the short-term dynamics of detrended possum abundance in a separate paper.

METHODS

Study area

The study area (41°21'S, 174°58'E) lies in a steep-sided valley 10 km from the sea in the Rimutaka Range in the southern North Island of New Zealand (Fig. 1). The site was called "Area A" by Bell (1981) and Cowan and Waddington (1990) and the "Station grid" by Brockie (1982). To the north and west the trapping grid is bounded by the shingle beds of the Orongorongo River and its tributary, Greens Stream. Four private huts and the buildings of the Landcare Research (formerly DSIR) field station lie within the study area, but the huts are occupied for only a few weeks each year and we believe that people locally have little effect on the possums. Possums were protected in the study area. Bovine tuberculosis *Mycobacterium bovis* was absent from the population with the exception of a single known case in 1985 (Brockie *et al.* 1987).

Most of the trapping grid is in mixed podocarp/hardwood forest on a consolidated fan of Pleistocene gravels at an elevation of 100–120 m, and sloping gently to the north. Part

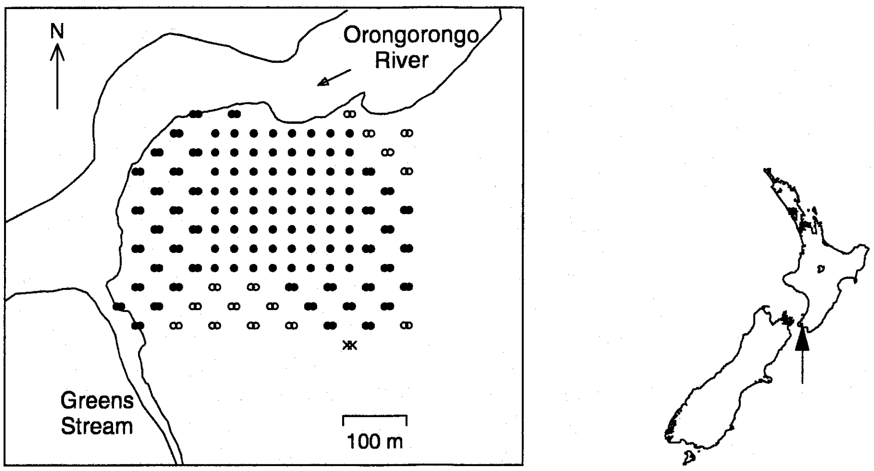

Fig. 1. Orongorongo Valley possum trapping grid as operated from 1970 to 1995. Single-cage trap: •; double-cage or two single traps: • • 1970–1995, OO 1980–1995 only, xx 1970–1979 only. From 1996 to 2002, single traps were placed evenly at 30 m spacing throughout the 1980–1995 area.

of the grid includes a stand of kanuka *Kunzea ericoides* on a younger terrace on the bank of Greens Stream, a swampy area overtopped by *Freycinetia banksii*, and beech forest *Nothofagus truncata* and *N. solandri solandri* on the hill slopes to the south and east. Plant nomenclature follows Allan (1961) and Connor and Edgar (1987). Two small streams dissect the fan.

The mixed forest covering most of the trapping grid has a complex multi-layered structure (Fitzgerald 1976). Scattered *M. robusta* and *Dacrydium cupressinum* over 30 m high emerge above a canopy at 6–20 m comprising *Elaeocarpus dentatus, Laurelia novae-zelandiae, Melicytus ramiflorus, Hedycarya arborea, Knightia excelsa, W. racemosa, Schefflera digitata,* and *Pseudowintera axillaris,* as well as tree ferns *(Cyathea* spp. and *Dicksonia squarrosa*). Epiphytes (*Astelia solandri, Collospermum hastatum,* and *Griselinia lucida*) are abundant, and are used frequently by possums as daytime refuges (Ward 1978; Cowan 1989a). Lianes are common, and two (*Metrosideros fulgens* and *Ripogonum scandens*) are seasonally important possum foods (Fitzgerald 1976; Allen *et al.* 1997). Except for the stony riverbed and local areas of erosion at higher altitude, a mosaic of similar habitat was continuous for several kilometres around the trapping grid.

Rainfall at the field station averaged 2 505 mm per annum over 17 years and was fairly evenly distributed throughout the year with a slight winter maximum; mean air temperature was 15.9°C in summer (December-January) and 7.5°C in winter (June-August). Frosts were rare (Campbell 1984).

Trapping

Possums were caught in wire mesh traps set on the ground and baited with pieces of apple coated in flour mixed with a few drops of aniseed oil. Traps were checked and rebaited daily. Two types of trap were used: single-cage traps (the majority) and double-cage traps consisting of two compartments back-to-back, each with its own door and treadle mechanism.

In 1966–1968, traps were set on irregular lines (Crawley 1973). In 1969 permanent sites were marked on a 30 m grid over the whole area previously trapped. Paired single traps were used at 30 m or 60 m spacings on this grid from March 1969 to April 1970, but mostly only on a small central area (150 × 150 m). In May 1970, a permanent inner grid of 64 single traps was established at 30 m spacing on the central 210 × 210 m area (Fig. 1; Bell 1981). The remainder of Crawley's 1966–1968 study area was trapped from June 1970 to November 1979 with a double-cage trap at every second permanent site (i.e., 42 m apart). In February 1980, this outer grid was extended slightly to surround the inner grid except where it reached the river bank (Fig. 1). From February 1996, the paired traps on the outer grid were replaced with single traps at 30 m spacing, giving almost uniform coverage across the whole grid.

The frequency of trapping varied from year to year and between different parts of the grid. Because these variations constrained the analysis and interpretation of the data, we describe them in some detail. Crawley (1973) trapped "for three or four nights at approximately fortnightly intervals from February 1966 to October 1968 inclusive" on the central and eastern part of the study area, but only at 3-monthly intervals in the western part. The central "210 m" grid was trapped on at least one night in most months from May 1970 to December 1982 inclusive. Monthly trapping sessions consisted of four consecutive nights in 1970–1973, but usually only one night per month thereafter. The "outer" grid (42 m spacing) was trapped for three–four nights, one to four times per year from June 1970 to November 1979. From February 1978 onwards, these sessions coincided with trapping on the "210 m" grid, which was increased to four nights in those months.

From February 1980 to September 2002, the "extended" grid, including the inner "210 m" grid, was trapped three times each year. Trapping sessions were timed to sample critical points in the annual cycle: late February when young of the previous year were first readily trapped but not yet dispersing, late June at the end of the autumn birth pulse, and late September when pouch young were large enough to ear tag but were still caught with their mothers. Traps were set for 4 to 10 nights over a period of up to 14 days at each session. After 1979, trapping was occasionally interrupted in wet weather because the return for effort was poor and to avoid unnecessary stress to possums in the traps; a session then comprised two or three short runs of consecutive trapping nights.

Total trapping effort (trap nights per year) varied annually by a factor of almost four, and the proportion of all trapping conducted on the central "210 m" grid varied between 37% (1982–2002) and 86% (1974). Mark-recapture estimates of capture probability varied with trapping effort, but were generally high (>50%) (Fig. 2).

Handling and marking

On initial capture, possums were marked individually with a numbered tattoo and tag in opposite ears (Crawley 1973; Bell 1981). At each subsequent capture, possums were identified, weighed to the nearest 50 g and released at point of capture. Possums were immobilized for marking, measurement and pouch examination,

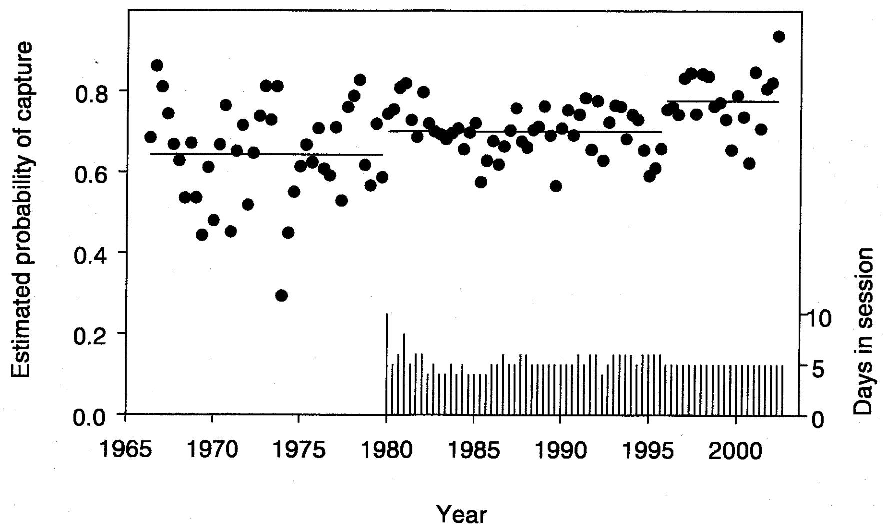

Fig. 2. Mark-recapture (Jolly–Seber) estimates of capture probability per trapping session 1966–2002, and number of days on which traps were set in each session 1980–2002. Horizontal lines indicate mean capture probability for periods over which the trap layout was essentially constant (1970–1979, 1980–1995, 1995–2002).

by an intramuscular injection of succinylcholine hydrochloride ("scoline"; Taylor and Magnusson 1965) or, after January 1980, by exposure to ether vapour in a closed box. Head length was measured with calipers to the nearest 1 mm; total length to the nearest 5 mm with a flexible tape along the back from nose to tail tip; and tail length similarly except that the tail was held at an angle to the back to define its origin. Adult females were measured each time they were immobilized for examination of their pouch in winter each year. Adult males were seldom remeasured before 1980, but from 1980 all males caught in February were immobilized and measured.

Occasionally animals died during trapping. Twenty-two possums died after injection of scoline in 1966–1979 and 20 died under ether anaesthesia in 1980–2002; these animals were treated in the Jolly-Seber analysis (below) as "removed on capture". A further 162 possums were found comatose or dead in the traps, or were weak when released and later found dead. These deaths were highly seasonal, occurring at a rate of 0.5–1.5% of all captures in June to October and at 0.1–0.3% outside these months (Efford 1991). Although stress related to trapping was clearly a proximate factor, most of these animals were so emaciated that they were likely to have died soon whether they had been caught or not. Expressed as a proportion of the estimated population, 0.6 ± 0.15% of animals per annum died directly as a result of handling, and a further 2.4 ± 0.43% died in some way associated with trapping. Anaesthetic deaths were high (>1.0%) in the first four years (1966–1969) and in 1977, 1981, 1998, and 1999.

Possums were killed by unauthorized trapping on the grid between June and September 2000. Ten bodies were found, but the actual number may have been higher.

Density estimation

Each of the intensive trapping sessions in 1980–2002 provided sufficient closed-population data for us to estimate density by fitting a spatial detection function using simulation and inverse prediction (Pledger and Efford 1998; Efford 2004). This new approach to density estimation avoids many of the problems of conventional methods while not requiring special trap layouts (cf Otis *et al.* 1978; Borchers *et al.* 2002). A spatial detection function g relates an animal's probability of capture in a particular trap to the distance between its home range centre and the trap. A half-normal curve was used here for g, although a step function gave very similar density estimates. Mark-recapture statistics (the closed population estimate $\hat{N}$, capture probability $\hat{p}$, and mean recapture distance $\hat{d}$ were modelled as the joint outcome of a complex sampling process specified by the population density D, the detection function g, and the trap layout T:

$$(\hat{N}, \hat{p}, \hat{d}) = F(D, g, T) + \varepsilon.$$

The function F was unknown, but it could be approximated by fitting a linear model to simulated realizations of the sampling process for a given trap layout and initial parameter values (D, $g(0)$ and σ_g). Density was estimated by applying the inverse function F^{-1} to field data ($\hat{N}$, $\hat{p}$, $\hat{d}$). The jackknife estimator was used to obtain $\hat{N}$ and $\hat{p}$ (Burnham and Overton 1978). Mean recapture distance $\hat{d}$ was estimated from recaptures within each trapping session. The method has been described in more detail elsewhere (Efford 2004). Software is available from the first author.

In order to assess trend over the entire series we estimated population size N_{JS} by the Jolly-Seber method (Seber 1982; Pollock *et al.* 1990). The seasonal data for each year before 1980 were pooled to give three notional trapping periods ("spring" (September–December), "summer" (January–April) and "winter" (May–August)), which matched the later periods of intensive trapping. Recaptures within a period were ignored, as were young carried by their mother. Jolly–Seber estimates could not be calculated for the first (February 1966) and last (September 2002) trapping sessions, and we chose to omit the whole of 1966 and 2002 from time series analyses to avoid the strong negative bias from heterogeneous trappability in these samples (Gilbert 1973).

We obtained population density by dividing the estimated population size by an "effective trapping area":

$$\hat{D}_{JS} = \hat{N}_{JS}/A_W.$$

Inverse prediction provided nearly unbiased estimates of density $\hat{D}_{IP}$ for 1980–2002 and from these we inferred the effective trapping area for this period

$$A_W = \hat{N}_{JS}/\hat{D}_{IP}.$$

The average A_W over 1980–2002 (20.6 ha) represented the area enclosed by the outermost traps (15.4 ha) plus a strip of width 64 m where the grid was not bounded by riverbed. A smaller area was enclosed by the traps set in 1966–1979 (12.2 ha) (Fig. 1); the effective trapping area with a 64 m boundary strip was then 18.0 ha. These adjustments served to correct for the change in trapping grid in 1980 and for bias in $\hat{N}_{JS}$ relative to $\hat{N}_J$. They do not allow for variation in movements over time.

Statistical analysis of trend

We required a simple statistical model to describe long-term trend in possum density. Examination of partial autocorrelation plots showed the residuals from preliminary models to be significantly autocorrelated and serial correlation of residuals may seriously bias the apparent precision of estimates from statistical trend models (e.g., Hurlbert 1984; Edwards and Coull 1987; Bence 1995). We removed some but not all of this effect by averaging the three seasonal estimates to give a single mean annual density for each year 1967 to 2001. Polynomial trend models were then fitted to the annual data by restricted maximum likelihood with the S-Plus function "gls", which can include an autoregressive error structure (Mathsoft 1999; Venables and Ripley 1999). The order of the error autoregression was chosen by selecting the quadratic trend model that minimized Akaike's information criterion; a second-order process was selected (AR(0) AIC = 127.8; AR(1) AIC = 126.1; AR(2) AIC = 123.7; AR(3) AIC = 123.7).

Polynomial trend models of varying order were compared by Akaike's information criterion. Smoothing splines, a family of more flexible trend models, were also fitted, using the S-Plus function "gam" (Green and Silverman 1994; Venables and Ripley 1999). Their smoothness was controlled by setting the equivalent degrees of freedom to the maximum beyond which there was no significant reduction in deviance. The fit of the smoothing spline model could not be compared directly with the polynomial models as "gam" does not allow for serially correlated errors, but graphical comparison was informative.

Transforming densities to logarithms produced qualitatively similar results in all analyses and for clarity we report only analyses on untransformed data.

Statistical analysis of body weight and biomass

Population biomass was estimated as the product of $\hat{D}_{JS}$ and the mean weight of all animals caught. Biomass was calculated separately for each sex and summed. Detailed analyses of body weight were restricted to animals known to be at least two years old. Weights of females carrying a suckling pouch young were adjusted by subtracting the weight of the pouch young, usually estimated from its head measurement using standard growth curves (M. Efford, unpubl. results). Trends in biomass and the annual mean body weight of each sex were analysed using methods similar to those described above for population size. However, allowing for autocorrelated residuals did not reduce the Akaike's information criterion of trend models for weight and we therefore used ordinary least squares. Throughout this chapter we express results as mean ± SE.

RESULTS

Population density

The seasonal population densities over 1967–2002 are plotted in Figure 3. An approximate periodicity of four years was apparent after 1979 in both the Jolly-Seber and inverse prediction estimates (peaks in 1983/4, 1986, 1990, 1995 and 1999). The amplitude of these fluctuations (mean($\hat{D}_{IP}$) in peak year ÷ mean($\hat{D}_{IP}$) in year of preceding trough) varied about a mean of 1.45 ± 0.09.

Annual population density varied within a relatively narrow band over the 35 years of the study (D_{JS} 6.5–13.7/ha; mean 9.76 ± 0.26/ha) and the overall linear trend (+0.039 ± 0.025/ha/year)

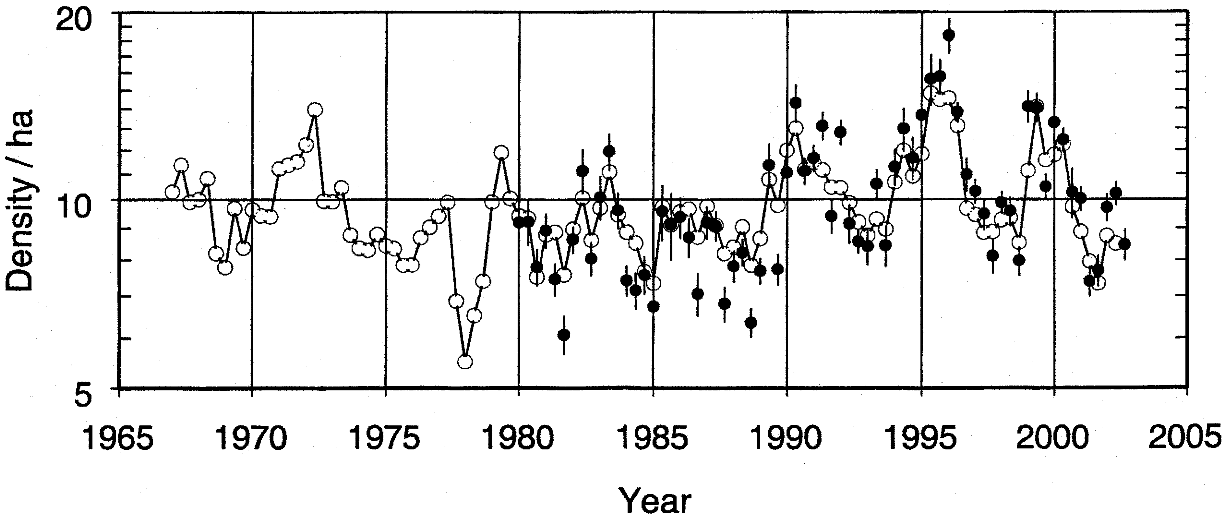

Fig. 3. Possum population density on a 20 ha study area in the Orongorongo Valley, Wellington, New Zealand, 1967–2002. Mark-recapture estimates by two methods: Jolly-Seber o and inverse prediction • ± 1 S.E. Density is shown on a log scale.

was not significantly different from zero (P = 0.13). However, annual density exceeded 11/ha only early in the study (1971, 1972) and in the last 10 years, suggesting a curvilinear trend (Fig. 4a). This was modelled with a fourth order orthogonal polynomial (Table 1). Of the non-parametric models, a spline smoother with four equivalent degrees of freedom provided the best fit. The fitted curve from this model closely tracked the fourth order polynomial (difference less than 0.5/ha) except in 2001 when it exceeded the polynomial by 1.1/ha.

Estimates of density from inverse prediction in 1980 to 2002 were more reliable than Jolly-Seber estimates because they allowed for temporal variation in possum movements. The preferred trend model for annual density over these 23 years was cubic (linear Akaike's information criterion = 94.1; quadratic Akaike's information criterion = 94.9; cubic Akaike's information criterion = 83.4). The overall linear trend was positive (+0.16 ± 0.052/ha/year). The linear trend in the Jolly-Seber estimate over 1980–2001 was +0.11 ± 0.032/ha/year.

Body weight and biomass

Mean annual body weight of adult males (2 306 ± 17 g) exceeded that of adult females (2 199 ± 21 g). In each sex there was only weak evidence for an overall negative linear trend in body weight (females: -3.4 ± 1.8 g/year, P = 0.07; males: -3.0 ± 2.0, g/year, P = 0.06). The best polynomial trend model for weight, selected by the criterion of minimum Akaike's information criterion, was a quadratic for males and a cubic for females.

Biomass density of the population combined estimates of density and mean body weight. As with total population size, the trend was curvilinear, and increasing from 1980 to at least 1995 (Fig. 4b). There was no overall linear trend in biomass (P = 0.14).

Table 1. Comparison of orthogonal polynomial trend models fitted to variation in annual mean Jolly-Seber possum density, 1967 to 2001. Each model includes a second-order autoregressive error term to account for serial correlation of residuals. Models fitted by restricted maximum likelihood, except for calculation of Akaike's information criterion when maximum likelihood was used (Venables and Ripley 1999). The quartic model minimized Akaike's information criterion.

Model	Autoregressive coefficients ϕ_1	ϕ_2	R^2	Akaike's information criterion
Intercept only	0.503	-0.325	–	128.4
Linear	0.485	-0.338	0.020	128.4
Quadratic	0.420	-0.398	0.070	127.1
Cubic	0.365	-0.462	0.180	122.2
Quartic	0.277	-0.542	0.291	115.4
Quintic	0.295	-0.532	0.269	117.4

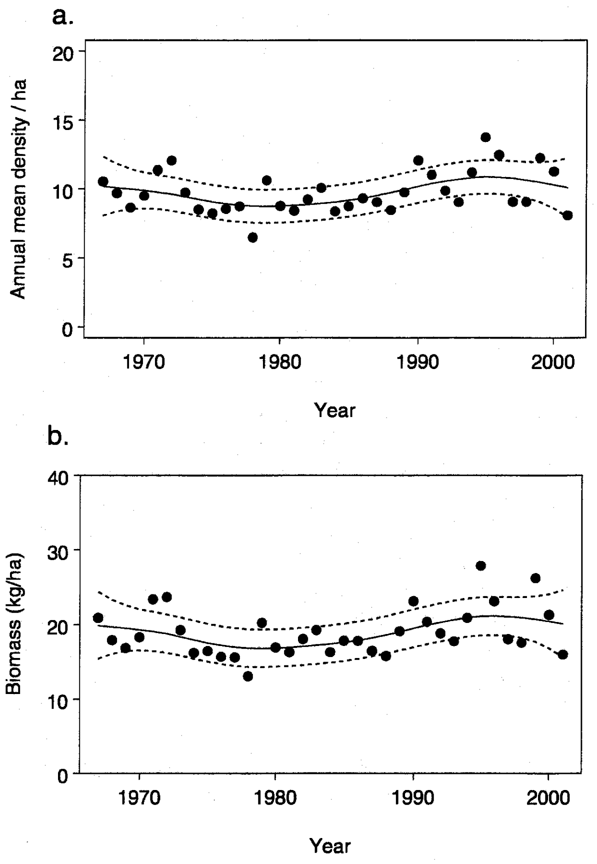

Fig. 4. Annual mean population density and biomass density during 1967–2001. The trend line shows the fit of a non-parametric smoother spline with four equivalent degrees of freedom; dotted lines indicate approximate 95% simultaneous confidence intervals for the mean. a. Annual mean population density, b. Annual mean biomass density.

DISCUSSION

Our mark-recapture analysis indicated a long-term fluctuation in the average density of the Orongorongo possum population, including an increase of about 3/ha since 1980, with superimposed short-term fluctuations. We consider the reliability of this result before placing it in historical and ecological context.

Should we trust the measured population trend?

Mark-recapture statistics to estimate density are notoriously sensitive to breaches of their assumptions (Otis *et al.* 1978; Pollock *et al.* 1990). For the period 1980–2002 we used a novel inverse prediction method that combines a robust closed population estimator (Burnham and Overton's (1978) jackknife) with simulation. Field trials lead us to believe this method performs well for possums (Efford, Warburton and Coleman, unpubl.), but further testing is needed to confirm its robustness to home-range differences between individuals and to short-term alteration of behaviour by trapping. A major advantage of inverse prediction is that it allows for temporal variation in the mobility of individuals, and hence in the effective trapping area. However, the trapping regime in the early part of the study (1966–1979) did not suit that method and for long-term trends we relied instead on an estimate of effective trapping area using a constant boundary strip width estimated from the inverse prediction estimates in 1980–2002. Trends in density may therefore have been an artefact of changing mobility of individuals. The 1980 change in trapping regime is particularly suspect because it nearly coincided with a change in the trend of the population. We do not believe the change after 1980 is an artefact because the new trend was sustained in both the Jolly-Seber and inverse prediction estimates after 1980, but we do not know how much of the variation in $\hat{D}_{JS}$ before 1980 was caused by varying home-range size.

Two minor sources of error must be acknowledged. Firstly, the density estimates for 1969 and 1974–1977 are likely to have been biased downwards because trapping intensity was then low, particularly on the outer, more widely spaced sections of the trapping grid. Secondly, the even placement of traps across the grid after 1995 caused a slight increase in the Jolly-Seber estimates, probably because it increased mean capture probability $\bar{p}$ and reduced CV(p). We determined an upper limit for this effect by recalculating the estimates of total density, having discarded data from alternate trap sites in the outer zone; the difference was +0.58 ± 0.09/ha in 1996–2002. The actual effect of the change would have been less than 0.58/ha because these calculations do not allow for the positive effect of captures in the second trap at each site in the earlier layout. Illegal hunting in 2000 caused the deaths of at least 10 animals (about 0.5/ha), which may have contributed to the low density in 2001. These details have negligible effect on the long-term patterns we report.

The study population increased over 1980–2001, a period of intensive live trapping (Fig. 2), and we have no cause to hypothesize a large, undetected, and negative effect of trapping as suggested by Clinchy *et al.* (2001). Some possums are known to have died in our study as a result of handling (see Methods), but we believe this effect was generally small relative to natural mortality. The population appears to receive more immigrants than it loses in emigration (Efford 1998), but such asymmetry is expected in a habitat mosaic, even for patches of "high quality" habitat (Watkinson and Sutherland 1995), and does not imply a disturbance of the natural regime by trapping.

Historical trends

Some aspects of the history of possum colonization of the Orongorongo Valley are known in reasonable detail while others must be interpolated. Figure 5 places our present data in historical context and suggests alternative scenarios where the interpolation is unconstrained.

Possums were liberated in 1893 by the Wellington Acclimatization Society at Wainuiomata, 10 km from the study area (Kirk 1920; Thomson 1922: 29). Pracy (1962) noted an earlier release by Abbott at Featherston (42 km away) in 1872, and further liberations in the "Southern Rimutaka Range" in 1894. Possums were trapped in the Orongorongo Valley for fur from about 1921 onwards (Mason 1958). Batcheler (1983) believed that possum numbers had peaked in the valley around 1940, but Campbell (1990) inferred from rates of spread observed elsewhere that possum numbers may have already been high in 1930.

Intensive kill trapping over 12 months from July 1946 to July 1947 was thought to have eliminated possums from a block of forest that included the study area (Mason 1958; Batcheler *et al.* 1967). We have been unable to reconcile the two published estimates of density from this removal trapping (11.0/ha Mason 1958; 6.4/ha Batcheler *et al.* 1967) except that they relate approximately the same numbers removed (1 024 and 1 031) to different reported areas (93 ha and 160 ha respectively). Mason (1958) mentions that 197 (19.2 %) of her sample were "kittens"; if these were dependent (pouch- or back-) young then they should be subtracted to obtain a density estimate directly comparable with the present series (8.9/ha). Immigration over the removal period may also have inflated the estimate.

Some possums were also killed in the study area for research purposes in 1953–1954, and occasionally over the following six years, although about 100 resident possums in the immediate vicinity of the field station were released alive and provided with supplementary food (Kean 1967, 1971, 1975; Kean 1958, unpubl. report). Kean (1971) considered that the population remained "essentially stable" at a density of about three per acre [7.6/ha], but the surviving data do not allow a precise estimate to be made. We believe that local population density returned to near carrying capacity before the present study began in 1966, as the general trend over the first 10 years was slightly downwards.

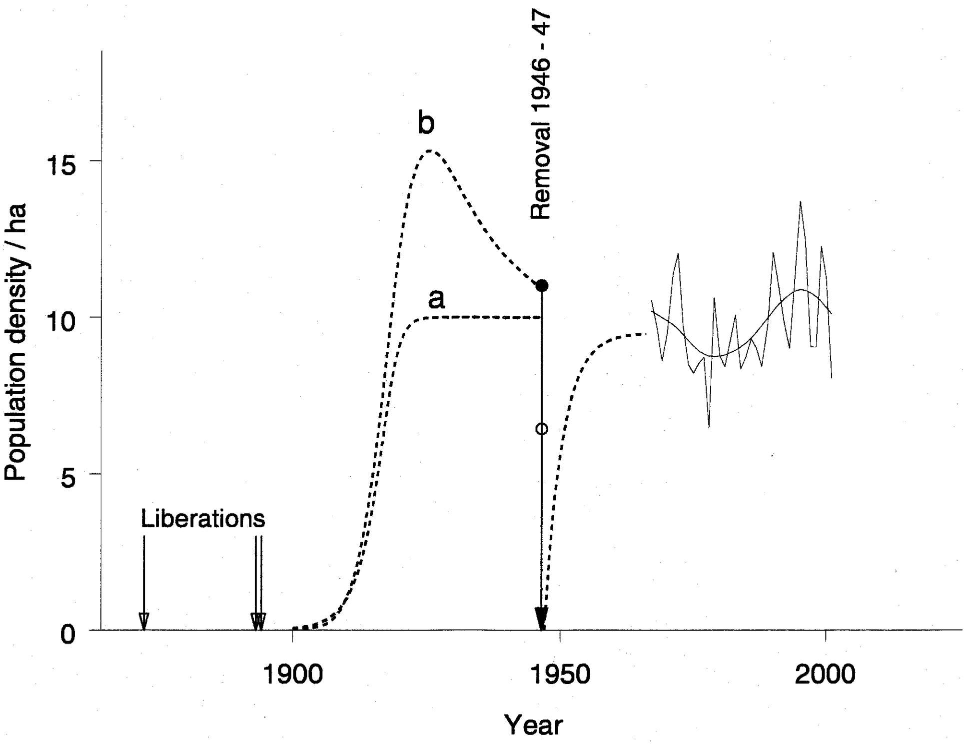

Fig. 5. History of possum density and carrying capacity in the Orongorongo Valley. Results for 1967–2001 are from the present study (annual mean density and smoothing spline). Known liberations were in 1872 (42 km), 1893 (10 km) and 1894 (probably <10 km). Alternative removal estimates of density in 1946–1947: • (Mason 1958) ○ (Batcheler *et al.* 1967) (see text). Dashed lines are hypothetical population curves assuming either low initial carrying capacity (a) or high initial carrying capacity (b) as described in the text.

We do not know exactly when possums first colonized the present site. We assumed for further calculations an initial density of 0.05/ha in 1900 (one colonizer per 20 ha), and constructed scenarios for low and high initial carrying capacity *K*. Under the "low-*K*" scenario this population reached, within 0.1/ha, an asymptote equal to the mean 1967–2001 population in 1924 (extrapolation with the discrete θ-logistic model of Barlow and Clout 1983; $\theta = 2$, $r = 0.3$, $K = 10$/ha). Alternatively, under the "high-*K*" scenario, population density may have reached an initial carrying capacity that was substantially higher than at present, and then declined. A plausible peak value is 18/ha, based on backwards extrapolation from the present series and the larger of the two 1946–1947 density estimates. Under this scenario the peak density would have been reached around 1927. The reconstructions are presented as smooth curves, but annual density presumably fluctuated around the trend curve as in later years. Values for r and θ in the model are uncertain, but of more concern is that we lack any local data to discriminate between the low-*K* and high-*K* scenarios. Mason (1958) reported that ". . . from information gleaned from trappers the density had been higher before the period of sample (1946–1947)", but this may merely have reflected year-to-year fluctuations and so does not contradict the low-*K* scenario.

The "declining carrying capacity" hypothesis

Our data refute the hypothesis of declining carrying capacity from 1967 to 2001. Average density tended to increase rather than decrease, especially from 1980 onwards when measurements were more precise. The amplitude of the overall variation in carrying capacity was small (9.7–11.3/ha, Fig. 4a), but it is clearly inconsistent with a downwards trend.

The hypothesis links three factors: tree mortality induced by possum browsing, declining food availability, and consequential effects on possum density. The role of possums in driving forest change is controversial (Veblen and Stewart 1982; Batcheler 1983; Campbell 1990; Bellingham *et al.* 1999; Nugent *et al.* 2001) and we cannot resolve it here. Instead we focus on the remaining factors, either of which may explain our failure to observe the predicted decline in possum density. Specifically, we ask whether changes in the forest reduced the food available for possums during 1967–2001.

Some tree species commonly eaten by possums in 1946–1947 (e.g., *Alectryon excelsus, Fuchsia excorticata*, and *Pseudopanax arboreus*) had become rare by the start of the present study (Mason 1958; Fitzgerald 1976; Campbell 1984, 1990). Three of 24 large *M. robusta* monitored on the possum study area from 1969 to 1974 died as a direct result of sustained possum browsing in 1974, but there has been no further mortality (Meads 1976; Campbell 1990; Cowan *et al.* 1997). *Weinmannia racemosa* and *Beilschmiedia tawa* on a central 2.25 ha plot suffered significant mortality between surveys in 1969 and 1994 (the number of *B. tawa* stems >100 mm DBH declined from 29 to 4, and of *W. racemosa* from 27 to 7; Campbell 1990; P. Knightbridge, pers. comm.). *Weinmannia racemosa* remained common in two areas outside the central plot but within the perimeter of the possum grid (Efford and Smith, unpubl. data) Most other tree and shrub species increased in stem density over 1969 to 1994, including some palatable species such as *Geniostoma ligustrifolium, Melicytus ramiflorus* and *Schefflera digitata*. The quantitative effect of these changes on the availability of food for possums is uncertain, but there may have been little net change in the availability of palatable foliage between 1967 and 2001.

Allen *et al.* (1997) documented changes in the composition of the leaf diet of Orongorongo possums between 1969 and 1989 by faecal analysis. *Weinmannia racemosa* and *G. ligustrifolium* both declined in relative importance, while *M. ramiflorus* and *Ripogonum scandens* increased. Foliage of *M. robusta* remained the single most important item of diet throughout and showed no detectable trend relative to other components.

Non-foliage plant parts (flowers, buds, fruit, bark) and fungi make potentially important contributions to possum diet (Fitzgerald 1976; Cowan 1989b, 1990b; Nugent *et al.* 2000, 2001). We lack data on long-term changes in the availability or consumption of these foods, with the exception of two canopy trees, *Elaeocarpus dentatus* and *Nothfagus truncata*. *Elaeocarpus dentatus* produces a variable annual crop of fruit that is eaten avidly by possums and has been linked to annual variation in breeding success (Bell 1981; Ramsey *et al.* 2002). *Elaeocarpus dentatus* was second only to *M. robusta* in aggregate basal area on the central 2.25 ha plot surveyed by Campbell (1990) in 1969, 1978 and 1985, although it was less common or absent towards the edges of our study grid. Our analysis of its annual fruitfall, estimated from collecting trays within the study area, showed no long-term trend ($P > 0.1$ for both linear and quadratic trend; unpubl. results).

Nothofagus truncata dominated the forest canopy on the southern and eastern edges of our grid, but it did not occur at all on Campbell's (1990) plot. Its seeding was monitored with collecting trays placed under selected trees from 1968 to 2002 (e.g., Fitzgerald *et al.* 1996). *Nothofagus truncata* flowers and fruits profusely only in "mast" years. Mast seeding (>500 seeds/m^2) occurred in 1971, 1979, 1986, 1990, 1995 and 1999. The 1971, 1979, 1995 and 1999 mast events coincided with four of the five largest seedfalls of *E. dentatus* in the same interval (the other was in 1968), and it is likely that flowering of both species is initiated in response to climatic triggers in the previous summer (Kelly 1994; Schauber *et al.* 2002). Radiotagged possums travelled hundreds of metres from their core ranges to feed on *N. truncata* flowers and fruit in 1971 (Ward 1978), and stomach analyses from South Island sites show that flowers and seed of other *Nothofagus* species are sometimes the main food of possums (Sweetapple 2003). A possible explanation for the general decline in possum density between 1972 and 1978 is that there was no major masting of either tree species in this interval.

In summary, we lack evidence for a major decline in either the foliage or non-foliage foods available to possums on the study area between 1967 and 2001. The slight negative trend in average body weight does suggest increasing nutritional stress. Low individual body weight may have demographic consequences in extreme years (e.g., breeding failure in 1996; Ramsey *et al.* 2002).

If food availability did not decline then it is unsurprising that average possum density did not decline. However, our data also show a clear increase in possum abundance over 1980–2000 which itself requires explanation. Nugent *et al.* (2001) argue that possum numbers are limited primarily by the digestible and nutritious non-foliage components of their diet, and that the lack of downwards trend in the Orongorongo Valley population reflects constancy, or possibly an increase, in the availability of these dietary components. This hypothesis is not excluded by our results, but we suggest here an alternative that should be considered. Turning the original argument on its head, we speculate that the foliage availability of some opportunist species eaten by possums, such as *M. ramiflorus* and *R. scandens*, may have actually increased over time and driven an increase in average possum density. Palatable opportunist plant species may increase in the face of browsing by possums if they are sufficiently fast-growing and resilient, with the result that possum carrying capacity is buffered against the loss of less resilient palatable species. This hypothesis suggests that the response of a plant species to possum browsing is determined jointly by its palatability to possums, its growth response when browsed, and its response to indirect effects such as possum-induced mortality of competing species (see also Nugent *et al.* 2001). Site characteristics (e.g., fertility) may affect all three of these components; variation in the response of plant species to possum browsing is therefore to be expected (e.g., *F. excorticata*, Sweetapple and Nugent 1999).

Vegetation turnover in New Zealand forests is driven by many factors other than herbivore impacts (e.g., Bellingham *et al.* 1999). The vegetation of the Orongorongo Valley in particular has been strongly influenced over the last 150 years by earthquake and storm events with long-lived effects on geomorphology and forest succession (Robbins 1958; Campbell 1984). Weather may also affect possums directly. For example, the time spent feeding is reduced on rainy nights (D. Ward, pers. comm.) and declining possum density on our study area coincided with seven years of above-average rainfall in 1974–1979. Experimental manipulation of possum browsing is required to control these confounding variables.

High and apparently stable possum densities (>15/ha) have been measured in pasture-edge forests containing abundant seral or opportunist canopy or subcanopy species (*M. ramiflorus, Muehlenbeckia australis, F. excorticata, Aristotelia serrata*) at Mt Bryan O'Lynn, Westland (Coleman *et al.* 1980) and at Pigeon Flat, Dunedin (Efford *et al.* 2000). Pasture species contribute to the diet at these sites and may thereby enhance local carrying capacity, although the importance of this effect has been questioned (Efford 2000). The floristic composition of these modified forests themselves is probably highly attractive to possums, and presence of the same seral species has been invoked to explain local possum abundance in *Nothofagus* forests that have been thought to offer little else for possums to eat (Owen and Norton 1995) but there is new evidence for consumption of *Nothofagus* flowers, seed and leaves (Sweetapple 2003).

If highly modified forests sustain possum densities that are equal to or higher than unmodified forests, then there is an even stronger argument than before to actively manage and retain forests in an intact state. High and fluctuating densities of possums in modified forests pose a continuing threat to secondary prey such as invertebrates and nestling birds.

Annual dynamics

We have focused on long-term trends in the mean density of the Orongorongo possum population. We interpret this as the "ecological carrying capacity" in Caughley's (1979) sense of an equilibrium density about which the population fluctuates. Here we have not sought to "explain" short-term variation in abundance such as the low in 1977 and the peaks in 1990 and 1996 (Fig. 3). Preliminary analyses (Efford 2004) show that population change is only weakly correlated with the available data on weather and fruiting of *E. dentatus*. Pulses of yearling recruitment occurred in some mast years, but not in all; the role of mast flowering by *N. truncata* has been overlooked previously and requires further analysis. The second-order autoregression of residuals from our trend model suggests delayed density dependence in the population time series that may be due to a short-term (1–2 year) plant-herbivore interaction. If this is so, then it will be necessary to distinguish two nested time scales of possum-forest interaction: one concerned with year-to-year dynamics, including the conventional topics of population limitation, cyclicity, and regulation, and one with longer-term shifts in carrying capacity such as we have shown.

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