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# BRUSHTAIL POSSUMS (*TRICHOSURUS VULPECULA* KERR) IN A NEW ZEALAND BEECH (*NOTHOFAGUS*) FOREST

**Summary:** Brushtail possums were studied over a period of four years by live-trapping, poisoning and kill-trapping on an altitudinal transect (455-1500 m a.s.l.) in beech *(Nothofagus)* forest in South Island, New Zealand. There was a single breeding season in autumn in which most females (including 80% of one-year-olds) panicipated. Trap-revealed ranges of adults were up to 1 km long and some immature males dispersed up to 10 km. Capture rates in live-traps were highest in beech/podocarp forest at 455-460 m a.s.l. and declined with altitude. No possums were caught above the treeline (1400 m a.s.l.). Removal of possums by poisoning on a 500 x 500 m grid yielded a density estimate of 0.46/ha in mixed beech forest at 460-650 m a.s.l. The density, weights, reproductive performance, movements and structure of the study population are compared with the results of other studies and some implications for possum control and fur harvesting are briefly discussed.

**Keywords:** Population dynamics; reproduction; movements; home range; weight; possum; *Trichosurus vulpecula*; Phalangeridae; Nelson Lakes National Park; Mt Misery; New Zealand.

## Introduction

Australian brush tail possums *(Trichosurus vulpecula* Kerr) were introduced in to New Zealand about 1840 and have subsequently spread throughout North and South Islands (Pracy, 1962). These nocturnal herbivores damage forests and carry bovine tuberculosis (Kean and Pracy, 1949; Julian, 1981), but they also form the basis of a fur industry which has recently earned about $20 million annually in overseas earnings (Clout and Barlow, 1982). The population ecology of brushtail possums has been extensively studied in both Australia (Dunnet, 1964; How, 1981) and New Zealand (Crawley, 1973; Bell, 1981; Brockie, Bell and White, 1981; Clout and Efford, 1984). However, none of these studies has examined the ecology of possums in beech *(Nothofagus)* forest, despite the fact that this vegetation type covers about 4.5 million ha (70% of all native forest) in New Zealand (J. L. Nicholls, pers. comm.).

This paper presents the results of a four-year study of the population ecology of possums on an altitudinal transect in a beech forest sequence in South Island, New Zealand. Possums were regularly live-trapped in the area for three years before being poisoned and kill-trapped to yield samples for density estimation and determination of population structure.

## Study Area

Our study was conducted on Mt Misery (41°56'S, 172°41' E), at the head of Lake Rotoroa in Nelson Lakes National Park, South Island, New Zealand. Possums invaded this area about 1960 (Pracy, 1974). Before our study, possums were sporadically trapped in the vicinity by commercial hunters, but this ceased with the start of our study.

An altitudinal transect was established on the mountain, running from 455 m a.s.l. at lake level to 1500 m a.s.l., just below the summit, sampling five major altitudinal zones which we distinguished by topography and vegetation. These zones were the alluvial flats, the fan slope, the main slope, the upper slope and the subalpine tops (Fig. 1).

The alluvial flats (455-460 m a.s.l.) at the foot of Mt Misery are covered with beech/podocarp forest with a canopy of *Nothofagus fusca** and N. *menziesii,* emergent *Podocarpus spicatus* and P. *dacrydioides,* a mixed understorey dominated by *Pseudowintera colorata* and *Coprosma rotundifolia,* and streamside vegetation including *Fuchsia excorticata*. The fan slope (460-650 m a.s.l.) has a canopy of N. *fusca* and N. *menziesii* with an understorey of *Weinmannia racemosa, Carpodetus serratus, Pseudopanax crassifolius, Coprosma rhamnoides* and C. *microcarpa* and areas of dense *Blechnum discolor*. The steep main slope (650-1100 m a.s.l.) also has a canopy of N. *fusca* and N. *menziesii,* but above 1000 m a.s.l. N. *solandri* appears in the canopy and N. *fusca* is less abundant. The upper understorey also shows zonation, with *Weinmannia racemosa* dominant below 700 m a.s.l. but replaced by N. *menziesii, Griselinia littoralis, Podocarpus hallii* and *Pseudopanax simplex* above this, with a narrow band of *Metrosideros umbellata* at about 750 m a.s.l. The lower understorey on the main slope contains *Coprosma microcarpa,*

*Botanical names follow Allan (1961).

*C. foetidissima* and *Cyathodes juniperina*. The upper slope (1100-1400 m a.s.l.) has a canopy and upper understorey dominated by N. *solandri* and N. *menziesii,* with the latter species uncommon above 1300 m. The lower under storey is also dominated by N. *solandri* and N. *menziesii,* but above 1300 m other species such as *Coprosma pseudocuneata,* C. *parviflora* and *Olearia lacunosa* are also present. The subalpine tops commence at the treeline (1400 m a.s.l.), where there is a narrow zone of subalpine scrub with *Dracophyllum uniflorum, Phormium cookianum, Cassinia* sp. and *Hebe* spp. Above the treeline the vegetation grades into subalpine tussock and herbfield, with *Chionochloa, Aciphylla* and *Celmisia* spp. covering the slopes and the large basin below the rocky summit.

Precipitation and temperature data were recorded monthly from May 1978 to August 1983 at sites on the alluvial flats (455 m a.s.l.) and subalpine tops (1500 m a.s.l.) of Mt Misery. Mean annual precipitation for the five year period was 2138 mm at the lower site and 2706 mm at the higher one. Mean monthly maximum temperatures ranged from 13.5°C (June) to 31°C (January) at 455 m a.s.l. and from 7°C (July) to 22 °C (January) at 1500 m a.s.l. Mean monthly minimum temperatures ranged from - 6.5 °C (July) to 4°C (January) at 455 m a.s.l. and from -9.5°C (August) to -0.5°C (January) at 1500 m a.s.l. (J. A. V. Tilley, pers. comm.).

## Methods

*Live-trapping*

Possums were live-trapped in treadle-operated cage traps spaced at 100 m intervals along the altitudinal transect at Mt Misery (fig. I). There were nin.e traps on the alluvial flats, nine on the fan slope, 12 on the main slope, 11 on the upper slope and l0 on the subalpine tops. The traps were set and baited with pieces of apple for three consecutive nights every three months from late May 1978 to late May 1981.

On first capture, all possums were immobilised by an intramuscular injection of succinylcholine chloride (Taylor and Magnussen, 1965), individually marked with numbered monel eartags and ear tattoos, weighed, measured, examined and released at the point of capture. On subsequent capture, adults were usually just identified, weighed and released, but breeding females were always immobilised to permit examination of the pouch and measurement of pouch young.

*Poisoning and kill-trapping*

Baits of commercially-produced soya paste impregnated with sodium cyanide were used to kill possums at Mt Misery in mid-June 1981. The baits were laid for four consecutive nights at 50 m intervals on a square grid which was marked out over a 500 x 500 m area of the fan slope (Fig. 1) and for three nights at 50 m intervals along the transect up to the treeline. Baits were not laid along that section of the transect which passed through the poisoning grid. All baits were laid on the ground and were checked and (if necessary) replaced each day. Poisoned possums usually died close to the bait and their carcasses were collected each day.

After this poisoning operation, the capture of possums in cage traps proceeded as before from late August 1981 to late August 1982. However, all possums caught during this period were killed.

Dead possums from the poisoning operation and kill-trapping were examined, weighed, measured and their left lower mandible was removed for age determination.

*Density estimation*

The maximum likelihood method of Zippin (1956) was applied to removal catch data from the fan slope grid to estimate the number of possums which were susceptible to poisoning of this area during 8-12 June 1981. To determine the effective poisoning area of the fan slope grid, those possums killed on the innermost 350 x 350 m part of it (containing 36 baits) were recorded separately. The method of Hansson (1969) was then used to calculate the width of boundary strip around the grid, by comparing the kill of possums on this inner zone with that on the whole grid.

*Determination of age and reproductive status*

Pouch young up to four months old were placed intO weekly age classes according to their head and tail measurements, using the nomogram of Lyne and Verhagen (1957). Poisoned and kill-trapped possums were aged from layers in the dental cementum of molar teeth (Pekelharing, 1970) and placed into annual age classes, assuming a birth date of 1 May.

The criteria of sexual maturity were invagination of the pouch for female possums and a testis length (measured through the scrotum) of

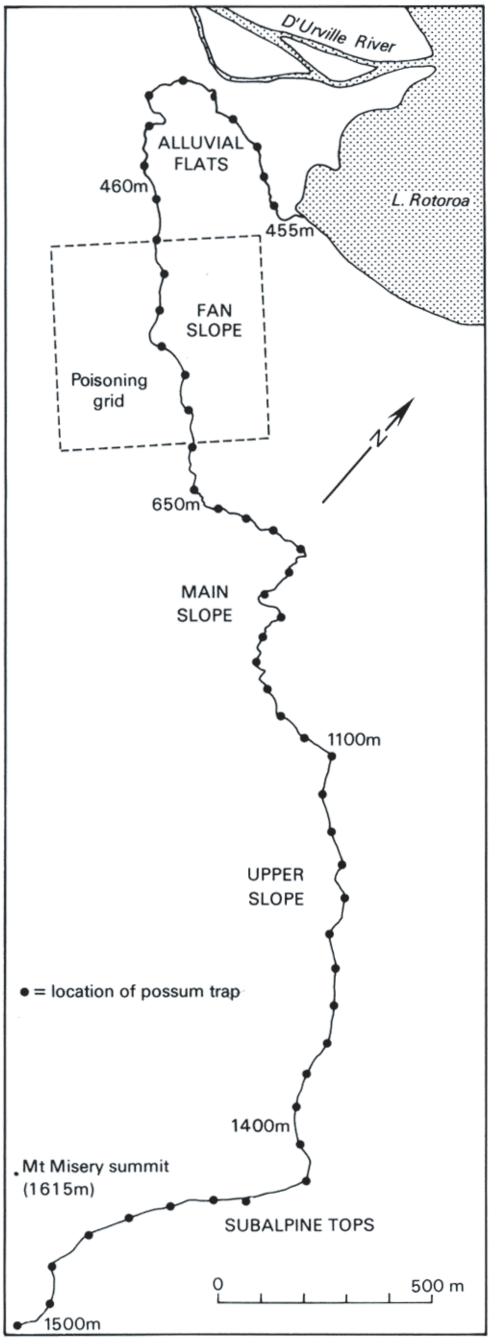


Figure 1: *The altitudinal transect on Mt Misery, showing distribution of possum traps and location of the 500* x *500 m poisoning grid on the fan slope.*

>18 mm for males (Tyndale-Biscoe, 1955; Gilmore, 1969).

Females were classed as breeders if they were carrying a pouch young or had a stretched pouch and enlarged mammary gland.

*Calculation of range length*
Minimum individual range lengths were calculated for those possums whose location was recorded five or more times, by both trapping and poisoning. Minimum range length was taken as the minimum (straight line) distance between the farthest locations of an individual within the study area, measured from a map (Fig. 1).

## Results

*Altitudinal distribution and population density*
From May 1978 to May 1981 70 different possums were independently captured 181 times on the Mt Misery transect. Total captures per trap declined with increasing altitude (Fig. 2) and no possums were caught in any of the traps set above the treeline. The strongest feature of this altitudinal distribution of possum captures was the high capture rate in beech/podocarp forest on the alluvial flats, compared with that elsewhere on the transect. This was also reflected in the mean number of different possums caught per trap (Table 1), which suggests that the higher capture rate was not merely caused by higher individual trappability on the alluvial flats. The drop in overall capture rate from main slope to upper slope was not repeated in the number of different possums caught per trap (Table 1). However the kill rate at poison baits set along the transect in June 1981 was higher on the main slope (0.16 possums/bait/night) than on the upper slope (0.08/bait/night), supporting the evidence of capture rates in suggesting that possums were less abundant on the upper slope. Kill rates at poison baits set on the alluvial flats and fan slope sections of the transect could not be compared with those on the main and upper slope because intensive poisoning on a gridded area of the fan slope removed some possums which used the alluvial flats and virtually all of the fan slope residents.

From 8 to 12 June 1981, 28 possums were killed at poison baits set out on the 500 x 500 m grid on the fan slope of Mt Misery (Fig. 1). The weather throughout this four-night period was settled and fine. Twenty-two possums were

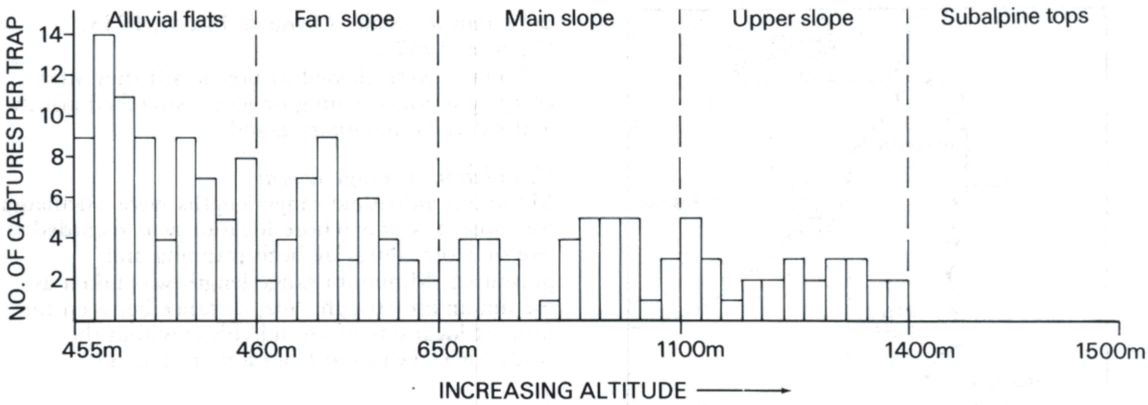


Figure 2: *Altitudinal distribution of possum captures on Mt Misery, showing number of captures per trap site from May 1978 to May 1981.*

Table 1: *Capture rates of possums in five different attitudinal zones on Mt Misery, May 1978 - May 1981. Possums caught in more than one zone were allocated to the zone in which they were initially caught.*

| Zone | Altitude (m a.s.l.) | Number of traps | Captures/ trap night | Individual possums/trap |
|---|---|---|---|---|
| Alluvial flats | 455- 460 | 9 | 0.214 | 3.11 |
| Fan slope | 460- 650 | 9 | 0.114 | 1.33 |
| Main slope | 650-1100 | 12 | 0.081 | 1.17 |
| Upper slope | 11 00-1400 | 11 | 0.065 | 1.45 |
| Subalpine tops | 1400-1500 | 10 | 0 | 0 |

poisoned on the first night, four on the second, and one on the third and fourth nights. These data yield a population estimate (Zippin, 1956) of 28.57± 1.53 possums in the local area, which is very close to the actual catch of 28. Included in this catch were nine marked possums which were known to frequent the fan slope. In subsequent kill-trapping along the transect (August 1981-1982) no other marked possums were caught on the fan slope, suggesting that this area was completely depopulated in June 1981.

Ten of the 28 possums poisoned on the 500 x 500 m grid were killed on the innermost 36 baits, encompassed by an area of 350 x 350 m. Assuming that possum density did not vary across the grid, we applied the method of Hansson (1969) to these data to yield a figure of 143 m for the distance beyond the grid boundaries which were affected by poisoning (i.e. the boundary strip). From this calculation the effective area depopulated by poisoning on the fan slope grid was 61.79 ha. Using the removal estimate of 28.57±1.53 possums inhabiting this effective area, we estimated that the density on the Mt Misery fan slope in June 1981 was 0.46± 0.02 possums/ha.

By assuming that the capture rate in live-traps bears a direct and constant relationship to local population density, the density of 0.46 possums/ha on the fan slope can be extrapolated to yield density estimates of 0.86/ha on the alluvial flats, 0.33/ha on the main slope and 0.26/ha on the upper slope.

*Reproduction*

The seasonal distribution of births, derived from measurement of 46 pouch young, reveals that possums at Mt Misery had a breeding season running from mid April to early July (Fig. 3). The main birth pulse extended into early May, with a subsidiary pulse in late May. All breeding females examined carried only one young.

The birth rate at Mt Misery was high and we found no evidence of pouch young mortality. All 17 of the females captured at the end of August (1978-82) had a pouch young, as did 25 (86%)

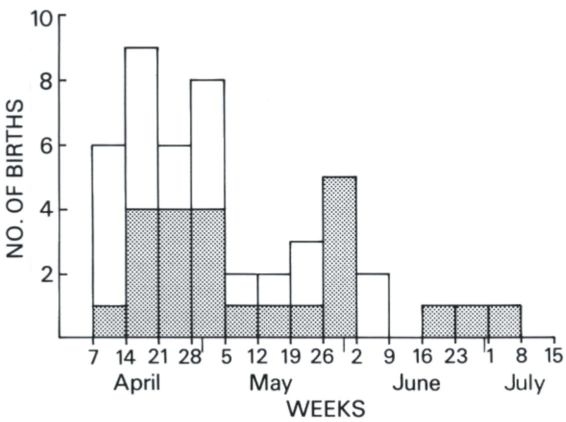


Figure 3: *Distribution of possum births on Mt Misery, in weekly classes, estimated from head and tail lengths of pouch young, using the nomogram of Lyne and Verhagen (1957). Hatched bars refer to pouch young of live-trapped females and unhatched bars to those of females poisoned in June 1981.*

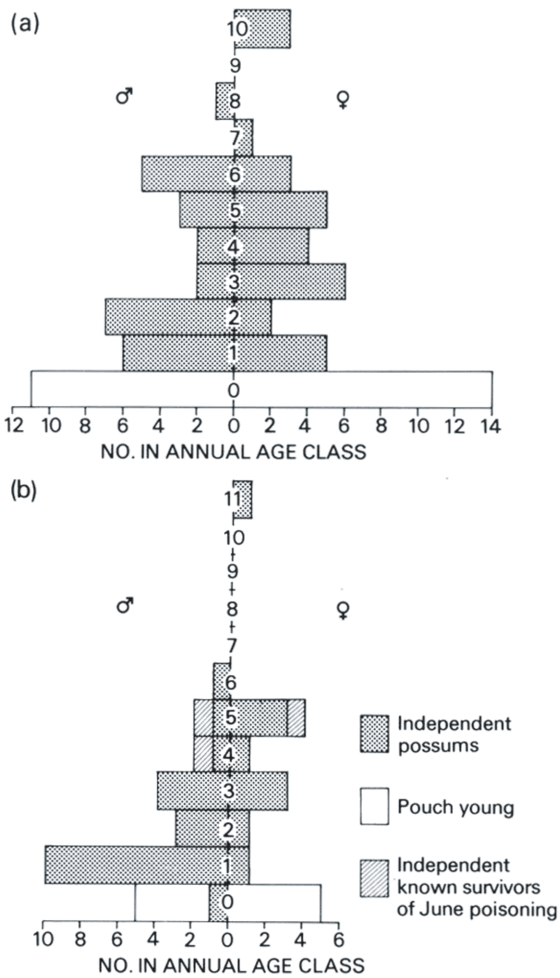


Figure 4. *Sex and age structure of possum samples from Mt Misery showing the distribution of animals by annual age classes. (a) The sample of possums poisoned in June 1981. (b) The sample of possums trapped and killed from August 1981 to August 1982.*

of the 29 females killed in mid-June 1981. Eight (80%) of the 10 one-year-old females examined between June and December (1978-82) had a pouch young or showed evidence (e.g. a stretched pouch) of having bred. The 2 non-breeding one-year-olds were both killed on 9 June 1981. These (and the two older, barren females killed at this time) could still have bred later that season, had they survived.

Male possums at Mt Misery matured later than females. Among males known (from their size and subsequent examination of tooth layers) to be between one and two years old, all four caught in May (12 months old), all six killed in June (13 months old) and all nine caught in August (15 months old) were immature. Three caught in November (18 months old) included one adult and two immature, and two caught in February (21 months old) were both adult. This suggests that males did not start to mature until they were about 18 months old.

*Population structure*

In mid June 1981, 55 possums were poisoned on Mt Misery. Twenty-seven of them (17 marked) were killed on the transect and 28 (nine marked) on the fan slope grid. These 55 individuals included 26 males and 29 females: a sex ratio which does not depart significantly from parity ($x^2$ = 0.04, P >0.5). The age structure of this sample of 55 animals (Fig. 4a) revealed a wide spread of ages, including three females more than 10 years old.

From late August 1981 to late August 1982, 34 possums were trapped and killed along the Mt Misery transect (including three marked survivors of the June 1981 poisoning operation which were caught in August 1981). The sample contained 23 males and 11 females, but this departure from parity was not statistically significant ($x^2$ = 3.56, p >0.05). The age structure of the post-poison sample of 34 possums (Fig. 4b) contrasts with the earlier age structure (Fig. 4a), especially in the proportion of one-year-old males. However, direct comparison of the two samples is invalid because they were collected in different ways over different time spans.

*Weights*

The weights of adult possums live-trapped in quarterly sessions from May 1978 to May 1981 averaged 3.24(± 0.41) kg for males and 3.03(± 0.37) kg for females, which were significantly lighter overall ($t = 3.14$, d.f. 137, $p < 0.01$). A seasonal trend in weights was indicated for both sexes (Table 2), with males apparently being heaviest in February and females in May.

Fifty-five possums poisoned on Mt Misery in June 1981 included 44 aged two years or more and 11 aged one year. Those aged two or more years were all adult, with male weights ($n = 20$) averaging 3.40(± 0.37) kg and female weights ($n = 24$) averaging 3.54(± 0.44) kg. The weights of one-year-old animals in this sample averaged 2.33(±0.18) kg for males ($n = 6$) and 2.42(±0.33) kg for females ($n = 5$). There was no weight difference between the sexes among either the older ($t = 1.11$, d.f. 42, $p > 0.2$) or younger ($t = 0.61$, d.f. 9, $p > 0.5$) possums in the June sample. The weight difference between possums live-trapped in late May (Table 1) and those poisoned in mid June was significant both for adult males ($t = 3.06$, d.f. 49, $p < 0.01$) and adult females ($t = 3.35$, d.f. 43, $p < 0.01$). The lighter weights of live-trapped animals were probably caused by them having empty stomachs by the time they were weighed.

*Movements*

This study yielded only sparse information on home range size, partly because trapping was conducted along a transect and partly because few individual possums were caught often enough to justify calculation of their range lengths. The nine adult males and six adult females which were captured five or more times had mean minimum range lengths of 529(± 303) m and 390(±316) m respectively, but there was no significant difference ($t = 0.86$, d.f. 13, $p > 0.4$) between the sexes in range length. Individual ranges about 1 km long were recorded for both males and females (Table 3) and some possums used up to three altitudinal zones on Mt Misery. For instance, the widest-ranging female possum had an apparently stable range which was at least 1034 m long, extending from the alluvial flats at 460 m a.s.l., across the fan slope, and up to 750 m a.s.l. on the lower part of the main slope.

Of the 24 (17 male, 7 female) possums first caught as juveniles on Mt Misery three were later

Table 2: *Mean weights (kg) of adult possums live-trapped in quarterly sessions at Mt Misery, May 1978 - May 1981.*

| | May (1978-81) | August (1978-80) | November (1978-80) | February (1979-81) |
|---|---|---|---|---|
| (a) Males | | | | |
| Mean wt. | 3.103 | 3.119 | 3.133 | 3.554 |
| S.D. | 0.334 | 0.340 | 0.456 | 0.381 |
| n | 31 | 17 | 12 | 25 |
| (b) Females | | | | |
| Mean wt. | 3.118 | 2.989 | 2.821 | 3.034 |
| S.D. | 0.405 | 0.360 | 0.491 | 0.251 |
| n | 19 | 12 | 7 | 16 |

Table 3: *Minimum individual range lengths (m) of possums on Mt Misery which were captured five or more times (including locations of animals poisoned in June 1981).*

| Males | | Females | |
|---|---|---|---|
| Captures (n) | Range length (m) | Captures (n) | Range length (m) |
| 5 | 266 | 6 | 264 |
| 5 | 310 | 7 | 238 |
| 5 | 341 | 7 | 238 |
| 6 | 314 | 8 | 276 |
| 6 | 467 | 10 | 1,034 |
| 6 | 889 | 12 | 287 |
| 7 | 291 | | |
| 9 | 920 | $\bar{x}$ =390±316 (S.D.) | |
| 9 | 966 | | |
| $\bar{x}$ = 529±303 (S.D.) | | | |

killed by fur trappers 3.5, 4.5 and 10 km up the D'Urville Valley from where they had last been trapped in our study area (Clout and Efford, 1984). All three individuals were one-year-old males which were still immature when they were killed.

## Discussion

*Comparison of population statistics*

The estimated density of 0.46 brushtail possums/ha in beech forest at Mt Misery is much lower than known densities (5.4-30.4/ha) in other types of native forest in New Zealand (Batcheler, Darwin and Pracy, 1967; Crawley, 1973; Coleman, Gilman and Green, 1980) or those prevailing in pine plantations (1-3/ha; Clout, 1977; Warburton, 1977) and scrubby pastoral land (1/ha; Jolly, 1976). There are no reliable estimates of brushtail possum densities in Australian *Nothofagus* forest, but in *Eucalyptus* woodland (Dunnet, 1964) and mixed forest (How, 1981) in eastern Australia their densities (<0.5/ha) are similar to that at Mt Misery.

The apparent decline in possum abundance with increasing altitude on Mt Misery is similar to the general pattern found by Coleman et al (1980) in podocarp-mixed hardwood forest at Mt Bryan O'Lynn (1218 m) in Westland. On Mt Bryan O'Lynn possum densities fell from 25.4/ha along a pasture margin (250 m a.s.l) to 1.9/ha on the mid-high altitude slopes (800-900 m a.s.l). However, numbers then rose again to 9.3/ha at the high altitude forest-scrub interface (900-1000 m a.s.l); a pattern which was not repeated on Mt Misery.

In size and reproductive performance, possums inhabiting the sequence of beech forest on Mt Misery compare well with those in podocarp-broadleaf forest of Orongorongo Valley near Wellington (Crawley, 1973; Bell, 1981). The average weights of live-trapped adults at Mt Misery were 3.24 kg for males and 3.03 kg for females, whereas comparable figures for Orongorongo Valley were 2.46 kg for males and 2.33 kg for females (Crawley, 1973). Despite this overall contrast, the seasonal pattern of weight variation was similar in both areas, with males apparently at their heaviest in summer and females in early winter. At both Mt Misery and Orongorongo Valley, possums had a well-defined season of births from April to June, with no second breeding season in spring. However, the annual production of pouch young per female in the Orongorongo Valley study area was only 0.71 (Bell, 1981), compared with at least 0.86 at Mt Misery, and the mortality rate of pouch young was 0.46, compared with zero at Mt Misery. The higher fecundity at Mt Misery was largely because at least 80% of females bred at one year of age, whereas in Orongorongo Valley fewer than 10% bred at one year and some not until they were three or four years old (Crawley, 1973; Bell, 1981).

Considering the low density, high weights and early maturation of possums at Mt Misery, it is interesting that we found no evidence of secondary spring breeding in this population. Spring breeding, in which some females give birth to a second young shortly after the autumn-born young vacates the pouch, has been recorded in several low density possum populations in both New Zealand (Gilmore, 1969; Boersma, 1974; Clout, 1977) and Australia (Dunnet, 1964; Smith, Brown and Frith, 1969). However, it does not occur in all low density populations (Clout, 1977; Warburton, 1977) and is probably more dependent on female nutrition at the critical time (and perhaps on early breeding in the preceding autumn; Bell, 1981), than it is on population density *per se*. The absence of spring breeding in the beech forest at Mt Misery might, therefore, reflect a relative lack of nutritious foods (e.g. fruit) in this habitat at the critical season.

Information on possum movements on Mt Misery is sparse, but nevertheless shows that some adults (of both sexes) had ranges c. 1 km long. These ranges were three times longer than any of those revealed by intensive live-trapping (Crawley, 1973) and radiotelemetry (Ward, 1978) of resident animals in Orongorongo Valley. Movements comparable with those occurring on Mt Misery have been revealed in only two other studies. Jolly (1976) twice recorded adult males moving 1.6 km across pastoral country to feed in orchards, and Green and Coleman (1981) found that resident possums on Mt Bryan O'Lynn regularly travelled up to 1.2 km through podocarp-mixed hardwood forest to feed on pasture. In both of these cases, possums were apparently drawn from one haL,itat type to another by the presence of particularly attractive foods. At Mt Misery, however, all movements were entirely within forest.

*Population composition*

The sex and age structure of the sample of 55 possums poisoned on Mt Misery in June 1981 was similar to other samples from relatively undisturbed populations (Brockie, Bell and White, 1981) in its equal sex ratio and distribution of ages to over 10 years. However, the sample of 34 animals trapped and killed from August 1981 to August 1982 contained twice as many males as females, and half of the males trapped were less than two years old. This apparently distorted population structure could result from a differential trappability of males and females, caused by a greater mobility and turnover of males in a local area, for example. However, there is now good evidence (Clout and Efford, 1984) that young male possums predominate among dispersers and, as a result, also predominate among the initial colonists of depopulated areas. Clout and Efford (1984) showed a very similar contrast in sex and age composition between undisturbed and recolonising populations in pine forest to that between the two samples of possums from Mt Misery. The apparent predominance of young males in the post-poison sample of possums from Mt Misery, therefore, was probably a real trend, resulting from dispersal into the partial vacuum created by the June 1981 poison operation and subsequent kill-trapping.

*Implications for control or harvesting*

The impact of possums on beech forest vegetation has not been studied to the same extent as their impact on other types of native forest in New Zealand. However, a recent study by Wilson (1984) at Mt Misery has shown that possums severely damage mistletoe *(Peraxilla* spp.) in beech forest and may threaten these plants with local extinction, even where possums are at low density. Wilson found that our poisoning of possums on Mt Misery in June 1981 reduced damage to mistletoe, showing that possum control in beech forest can measurably benefit the local flora. Unfortunately the benefit was short-lived and, despite kill-trapping, damage to mistletoe increased again in 1982 (Wilson, 1984). This example illustrates the likely difficulty of useful possum control in beech forest.

Our study shows that possums inhabit beech forest at relatively low density right up to the treeline, and that individual ranges in this habitat may exceed 1 km in length. Some young males disperse up to 10 km (Clout and Efford, 1984) and there is strong potential for rapid reinvasion of locall de o ulated areas. Useful control of possums in beech forest would need to be on an extensive (and hence expensive) basis, considering the distribution and movements of animals in this habitat. Local operations are unlikely to be successful unless careful consideration is given to the geographic isolation of controlled areas by natural boundaries.

The low density of possums in beech forest also makes this habitat relatively uneconomic for planned harvesting of possums for furs, despite the large size and good fur quality of the animals. Even if equilibrium densities approach l/ha in low-altitude stands, beech forest is still unlikely to yield more than 0.09 possums/ha/annum on a sustained basis (Clout and Barlow, 1982).

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