

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/262987916>

Home-range changes by brushtail possums in response to control

Article in *Wildlife Research* · March 2000

DOI: 10.1071/WR99005

CITATIONS

78

READS

151

3 authors, including:



Murray Efford

University of Otago

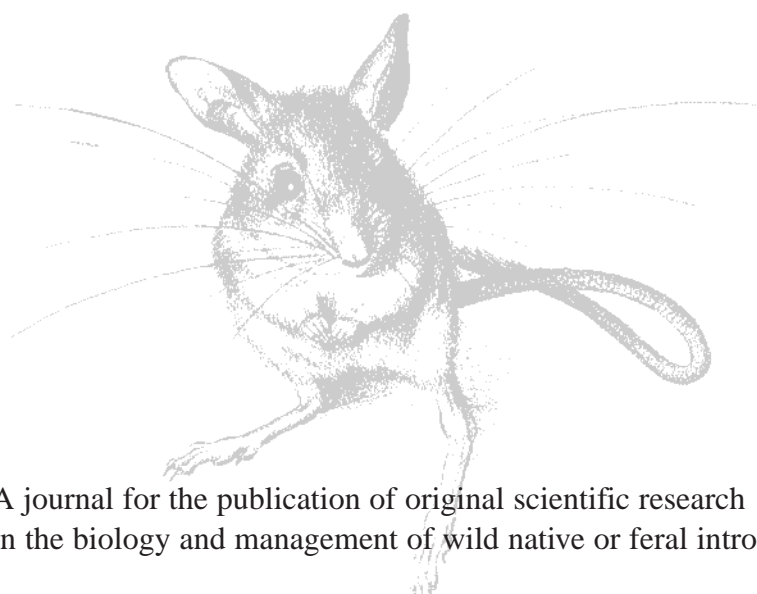
80 PUBLICATIONS 5,215 CITATIONS

SEE PROFILE

CSIRO PUBLISHING

Wildlife Research

Volume 27, 2000
© CSIRO Australia 2000



A journal for the publication of original scientific research
in the biology and management of wild native or feral introduced vertebrates

www.publish.csiro.au/journals/wr

All enquiries and manuscripts should be directed to

Wildlife Research

CSIRO PUBLISHING

PO Box 1139 (150 Oxford St)

Collingwood

Vic. 3066

Australia

Telephone: 61 3 9662 7622

Facsimile: 61 3 9662 7611

Email: david.morton@publish.csiro.au



Published by **CSIRO PUBLISHING**
for CSIRO Australia and
the Australian Academy of Science



Home-range changes by brushtail possums in response to control

Murray Efford^A, Bruce Warburton^B and Nick Spencer^A

^ALandcare Research, Private Bag 1930, Dunedin, New Zealand.

^BLandcare Research, PO Box 69, Lincoln, New Zealand.

Abstract. Common brushtail possums (*Trichosurus vulpecula*) are intractable pests in New Zealand. The effectiveness of local control can be limited by immigration, some of which has been attributed to a ‘vacuum effect’ – directed movements induced by the control itself. To characterise the vacuum effect we examined changes in the home ranges of trapped possums following control in a 6-ha block at one end of a 13-ha forest patch on farmland near Dunedin, New Zealand. We also monitored a sample of possums by radio-telemetry. After control, the density was 3 ha⁻¹ inside the removal area and 16 ha⁻¹ outside. During the year after the removal, 29% of possums within 100 m of the boundary of the removal area ($n = 38$) shifted their range centre at least 50 m towards it. The effect diminished rapidly with distance: only 1 of 28 animals moved more than 200 m from the boundary. The size of the previous range was a significant predictor of movement among males, but this may be partly a sampling artifact. We measured a net flux of 69 possums km⁻¹ across the boundary in the 12 months after control, and possums settled on average 44 ± 6.9 m inside the boundary. The vacuum effect in brushtail possums appears largely confined to home-range adjustments by individuals with ranges overlapping the area of reduced density. This limits its potential role in population recovery.

Introduction

The long-term effectiveness of pest control is limited by the rate of recovery of the pest population. Immigration of animals from surrounding uncontrolled areas is a potentially important mechanism of local population recovery. This influx may result from randomly oriented movements of individual animals, as in classical diffusion models, or from movements directed towards the areas of lower population density and higher *per capita* resources that exist after local control. Intuitively, a region of habitat in which density has been reduced represents an ecological ‘vacuum’ that will attract dispersing animals (e.g. Clout and Gaze 1984; Thomas *et al.* 1984). Here we use ‘vacuum effect’ to refer specifically to the result of such attraction, to differentiate it from dispersal that occurs independently of an induced density gradient.

Recolonisation of removal areas by immediate neighbours has been documented in several small mammal species – *Peromyscus leucopus* (Stickel 1946), *Microtus pennsylvanicus* (Van Vleck 1968), *Perognathus parvus* (Verts and Carraway 1986) and *Clethrionomys gapperi* (Schieck and Millar 1987; Nakata and Satoh 1994). The use of removal grids to monitor background rates of dispersal in small mammals has been questioned because measured immigration includes a ‘vacuum effect’ component, stimulated by the lowered density on the removal grid (Dueser *et al.* 1984; Boutin *et al.* 1985; Krohne and Miner 1985; Schieck and Millar 1987).

With only a few exceptions (e.g. Stickel 1946; Nakata and Satoh 1994), mammalian vacuum effects have not been investigated at the level of individual behaviour. It is intuitively likely that individuals move to maximise their access to resources when no longer constrained by the behaviour of neighbours. However, residents in some studies show great fidelity to their ranges even when apparently more favourable conditions exist nearby (e.g. Larsen and Boutin 1995). In order to understand the process of recolonisation we therefore require a more detailed understanding of the behavioural basis for vacuum effects.

Common brushtail possums (*Trichosurus vulpecula*) are a major introduced pest of New Zealand forests (Cowan 1990). These 2–4-kg arboreal folivores also threaten the dairy and beef industries in New Zealand by acting as a reservoir for bovine tuberculosis. Local populations sometimes recover after control much more rapidly than can be explained by *in situ* breeding (e.g. Clout and Efford 1984; Green and Coleman 1984; Thomas *et al.* 1995). The background rate of dispersal in undisturbed populations (e.g. Efford 1998) also appears inadequate to explain the observed rates of immigration after control, particularly immigration of adult females. A vacuum effect has therefore been suggested to account for higher than expected recolonisation rates of possums (e.g. Barlow 1993). Adult possums of both sexes occupy stable, broadly overlapping home ranges, and there has been little direct evidence for overt spacing behaviour (Green 1984). The vacuum effect hypothesis therefore raises questions concerning the underlying

Table 1. Population size and trappability of brushtail possums in a 13-ha forest remnant at Pigeon Flat, Dunedin, New Zealand

Minimum number alive (MNA) and Jolly–Seber estimates of population size (N) in August, 1994 to 1996. Also, number of captures per animal known to be alive in August, and mean Jolly–Seber estimate of capture probability p throughout each period

Period	MNA	Jolly–Seber estimates		Captures per marked animal	
		$N \pm \text{s.e.}$	$p \pm \text{s.e.}$	Range	Mean $\pm \text{s.e.}$
Pre-removal	208	211 ± 2.2	0.82 ± 0.018	1–33	12.7 ± 0.59
Post-removal, Year 1	129	134 ± 1.4	0.78 ± 0.018	1–24	10.9 ± 0.64
Post-removal, Year 2	134	142 ± 1.4	0.83 ± 0.020	1–24	11.5 ± 0.56

behavioural mechanisms, and the spatial scale and timing of the response.

In this study we attempted to induce vacuum effect dispersal of known resident adult possums by creating a neighbouring area of reduced density. If there is a vacuum effect then possums immediately adjacent to the removal area should increase their usage of the low-density area, and more distant animals from within the same patch should also move to exploit the increased *per capita* availability of resources.

Study area and Methods

The study site was a 13-ha semi-isolated remnant of native forest on farmland at Pigeon Flat near Dunedin, New Zealand ($45^{\circ}48'S$, $170^{\circ}32'E$). The forest was mostly low-canopy second-growth tree fuchsia (*Fuchsia excorticata*) and mahoe (*Melicactus ramiflorus*) with scattered broadleaf (*Griselinia littoralis*), and emergent miro (*Prumnopitys ferruginea*), rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*) and totara (*Podocarpus hallii*). Rows of macrocarpa (*Cupressus macrocarpa*) planted to shelter stock, and other irregular scrub remnants, radiated from the forest patch. Possums sometimes moved out from the forest to feed on the pasture.

Live-trapping

Cage traps ($n = 148$) were located throughout the forest on a 30-m square grid. The trapping grid was fully set for 6 nights in April–May 1993 and for 4 consecutive nights every 2 months from late July 1993 until October 1996. We baited traps with apple lured with flour and aniseed, and checked them each morning. Animals, when first captured, were anaesthetised with ether, weighed to the nearest 50 g, measured (head, total, and tail lengths; also testis length and width for males), and ear-tagged and tattooed. We judged females to be mature if they had a fully-formed pouch, and males if the length of a testis exceeded 17 mm.

Population estimation

The Jolly–Seber model was used to estimate population size (Seber 1982). Animals differed in trappability as shown by Carothers' (1971) test ($P < 0.001$). The size of the resulting downwards bias in the population estimates was estimated by simulation and inverse prediction, as described by Pledger and Efford (1998; see also Carothers 1979). For this analysis we assumed that individual trappability followed a beta distribution (a convenient 2-parameter distribution that was unimodal for the parameter values we observed: Johnson and Kotz 1970) and that population size was constant over the 8 trapping sessions before the removal. Despite the highly significant test statistic for heterogeneity, the estimated coefficient of variation in trappability was low ($20.8 \pm 3.7\%$) and the relative bias in the mean Jolly–Seber population estimate was correspondingly small (-3.3%).

Jolly–Seber estimates of the undisturbed population ranged from 193 ± 2 to 234 ± 4 in the pre-removal period (data from April 1993 to

August 1994) (Table 1). Females outnumbered males by $56 \pm 4\%$, but the two sexes showed the same population trends (Fig. 1). The trapped pre-removal population was stable except for seasonal recruitment between December 1993 and February 1994 as young of the previous breeding season became independent.

Several analyses, particularly the mapping of local distribution, could be performed only for known, marked individuals. Despite the known deficiencies of the 'minimum number alive' (enumeration) method (Nichols and Pollock 1983; Efford 1992), trapping was sufficiently intense that the enumerated population size approached the Jolly–Seber estimates. For example, at the time of the removal in August 1994 the Jolly–Seber estimate was 211 ± 2 and the minimum number alive was 208, including 23 individuals known to be alive but not caught in August 1994 (Table 1). Therefore, at least one trapping location was known for 99% of the Jolly–Seber population and 95% of the bias-adjusted population. Capture rates remained high throughout the study (Table 1).

We estimated local density by dividing the numbers of trap-revealed range centres in 30-m north–south bands parallel to the boundary of the removal area, by the area of each band. We also used the number of captures per trap ('trap success') for a more detailed index of local density. Trap success data were transformed to a linear density index by the method of Linn and Downton (1975). Traps that were disturbed (sprung or bait taken without catching a possum) comprised 15% of all settings and were treated in the calculations as a competing 'species' to remove any influence on the index of trap success.

Simulated control

Possums known to be resident in one end of the forest patch in August 1994 were removed to create a steep gradient in local possum density (Table 2). Possums were considered to be resident in the removal area if their previous trap-revealed home-range centres lay on or west of a north–south line approximately 150 m from the western end of the patch. In all, 80% of residents selected at random were targeted for removal. The percentage reduction was chosen to match a typical aerial control operation. A few radio-tagged females on the target list were replaced by other non-tagged females. The removal area was specially live-trapped on 19–22 August 1994 and target animals were humanely killed. Because fewer target possums than expected were actually caught, more residents were removed on 11–12 October 1994, relaxing the criterion that they were in the original random sample. The immediate effect of the removal was to create a step in average local density, from $3.1 \pm 0.35 \text{ ha}^{-1}$ in the removal area to $16.1 \pm 1.23 \text{ ha}^{-1}$ elsewhere. The density step was initially abrupt, at least as estimated by the previously documented range centres of survivors (Fig. 2a).

The trap success density index was at first approximately uniform across the trapping grid except towards the eastern end, where it dropped away (Fig. 3). After the simulated control, the index fell as expected in the controlled area; it also fell in the adjacent zone 0–120 m to the east (Fig. 3). Trap success remained high further to the east.

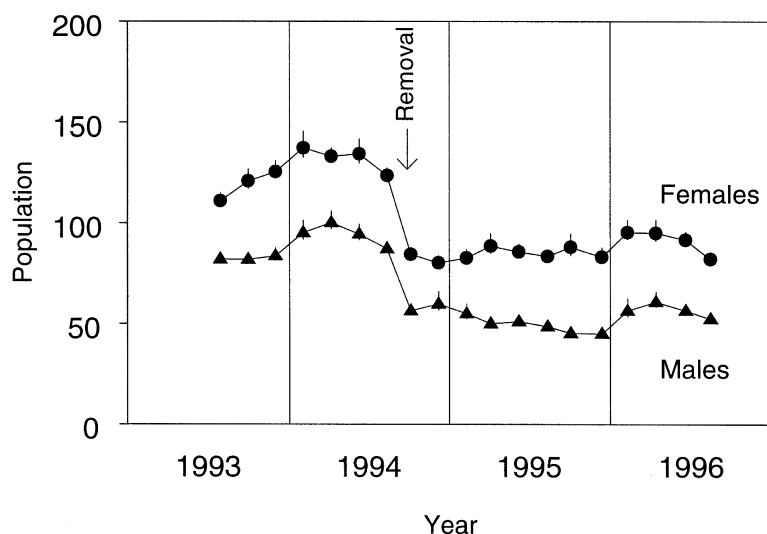


Fig. 1. Numbers of brushtail possums at the study area, as shown by bimonthly live-trapping over 3.5 years. Jolly-Seber population estimates and 95% confidence intervals. In total, 58 individuals were removed immediately after the August 1994 sample and a further 12 after the October 1994 sample.

Table 2. Possums experimentally removed from one end of a 13-ha study area near Dunedin, New Zealand

	Female		Male		Total
	Immature	Mature	Immature	Mature	
August 1994	4	31	6	17	58
October 1994	0	6	0	6	12
Total	4	37	6	23	70

Radio-telemetry

The availability of empty traps increased as a side effect of the simulated control in inverse relation to trap success. The resulting sampling bias towards the western end of home ranges that overlapped the removal area may have been sufficient to generate artifactual shifts in trap-revealed range centres. We tested this by comparing trap-revealed shifts with the change in home range revealed by night-time radio-telemetry. We used Sirtrack 2-stage possum transmitter collars (160 MHz band). The transmitter package weighed 23 g or <1% of average body weight (2.4 kg). Two null-peak aerial systems (Thomas 1982) were located at fixed sites approximately 200 m from opposite ends of the forest patch. Operators maintained radio contact, allowing nearly simultaneous bearings to be obtained. Foraging ranges were determined by tracking each animal hourly for 6 h after sunset on 4 consecutive nights each month between August 1993 and October 1996. This covered the nightly period of greatest activity (e.g. Ward 1978). Possums were tracked for an additional 4-night session (29 August 1994 – 1 September 1994) soon after the experimental density reduction.

Radios were attached preferentially to females as they were most critical to population recovery (e.g. Barlow 1993), and to animals trapped near the centre of the study area as they were most likely to respond to the removal. In all, 23 females and 3 males were tracked both before and after the removal.

Other statistical analyses

Trapping sessions were grouped for analysis into three approximately equal intervals: April 1993–August 1994 (pre-removal), December 1994–October 1995 (post-removal year 1) and December 1995–October 1996 (post-removal year 2).

Changes in home range between successive periods were tested for statistical significance using the multi-response permutation procedure

(MRPP) (Berry and Mielke 1983; White and Garrott 1990). The test is sensitive to changes in both home-range size and location. Home-range size was indexed by the mean deviation of capture locations (mean distance between the locations and the arithmetic range centre) for animals caught at least 3 times. This index has desirable statistical properties, including insensitivity to variation in the number of captures (Dice and Clark 1953; Tinkle and Woodward 1967). Radio-revealed home ranges were visualised by plotting the contour of the probability density surface that included 75% of fixes; the density surface was estimated by averaged shifted histograms (Scott 1985) with a quartic (biweight) kernel, bin width equal to 5 m and smoothing parameter 30 m.

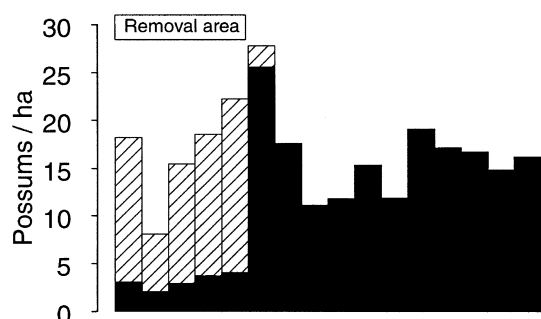
The locations (nominal 'centres') of individual home ranges were characterised by averaging the X- and Y-coordinates of all captures. Home-range shifts were summarised by the vectors connecting each animal's range centres in successive years. Range shifts were tested for uniform orientation against the alternative hypothesis of a westerly movement towards the removal area using the modified Rayleigh test (Zar 1996). Bearings are expressed in degrees east of true north.

We used logistic regression (Chambers and Hastie 1993) to investigate factors affecting the probability that individuals from outside the removal area moved towards it in the first year post-removal. For this analysis, animals were considered to have moved if they shifted their range centre at least 50 m to the west. Predictors were easting (perpendicular distance of the initial range centre from the removal boundary), sex (male or female), initial maturity (scored 'immature' if recorded immature at any time in the pre-removal period), average body weight at capture in the pre-removal period, and the 'mean deviation' index of initial range size. An initial model was fitted with all predictors as linear main effects. This model was refined by the stepwise addition of polynomial terms or removal of main effects using the S-Plus 'step.gam' function until there was no further reduction in Akaike's Information Criterion (AIC) (Chambers and Hastie 1993). Interactions were tested similarly. Particular effects were evaluated by comparing the associated reduction in residual deviance to a Chi-squared distribution with the relevant degrees of freedom.

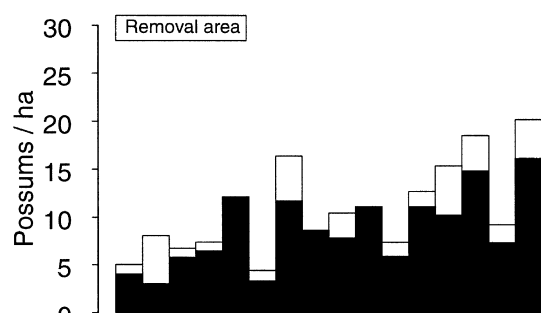
The spatial distribution of recruitment after the removal was analysed in relation to a north-south line 20 m east of the removal boundary that bisected the area. Range centres of about half the initial population lay on either side of this line (102 west, 106 east).

All calculations were performed in S-PLUS 3.3 for Windows (Statistical Sciences 1995) except for Jolly-Seber bias adjustments and MRPP, which used programmes written in Borland Pascal. Results are expressed as mean \pm s.e.

(a) Pre-removal



(b) 1 year post-removal



(c) 2 years post-removal

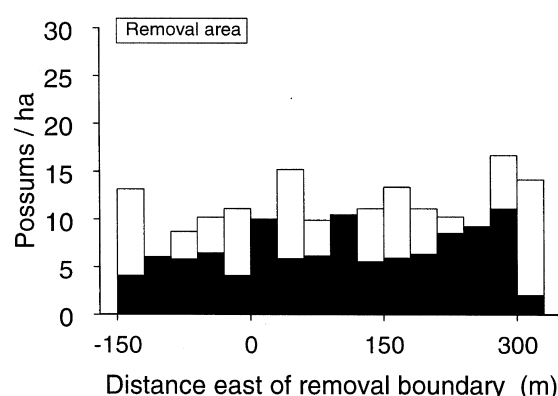


Fig. 2. Distribution of possum density in successive 30-m north–south bands across the experimental area, based on enumeration in August 1994–1996. The horizontal scale runs from west to east and its origin marks the approximate boundary of the experimental removal in August–October 1994. Hatched bars refer to animals removed in the experiment. Open bars are animals recruited to the marked population since the previous August.

Results

Population dynamics

The overall population estimate for each sex declined by about one third between August and December 1994 (females 35%; males 32%), mostly attributable to the simulated control operation (Table 2), although there was also natural late-winter mortality. Few young survived from the April 1994 birth pulse (unpublished data) and there was little net recruitment in the summer of 1994/95. Possum numbers remained static over the first year post-removal. Recruitment in the 1995/96 summer was similar to that in 1993/94, but there was still no net recovery of the population 2 years post-removal (Fig. 1).

Spatial pattern of density and recruitment after removal

The initial population showed no west–east linear trend in local density (slope = -0.002 possums $\text{ha}^{-1} \text{m}^{-1}$, $P = 0.78$). The removal created an overall west–east trend of 0.033 possums $\text{ha}^{-1} \text{m}^{-1}$ ($P = 0.005$). Captures in the first 12 months post-removal showed a reduced but still significant trend (0.022 possums $\text{ha}^{-1} \text{m}^{-1}$, $P = 0.005$), but in the second year post-removal the trend had virtually disappeared (0.010 possums $\text{ha}^{-1} \text{m}^{-1}$, $P = 0.10$).

In total, 38% of animals ($n = 133$) in the final (August 1996) enumerated population were first caught after the time of the removal in August 1994 and are assumed to have been immigrants or native recruits. There was little evidence of differential recruitment to the removal and non-removal area (Table 3) except that newly recruited native young tended to be more common in the non-removal area ($\chi^2 = 4.1$, d.f. = 1, $P = 0.04$; years pooled), as would be expected from the distribution of their parents after August 1994. The settlement of untagged recruits, which we presume mostly to be immigrants, was not significantly biased towards either area in the two years after removal ($\chi^2 = 2.4$, d.f. = 1, $P = 0.12$; years pooled). We are sceptical of the apparently significant 12:3 bias towards the removal area among untagged recruits in the second year ($\chi^2 = 4.3$, d.f. = 1, $P = 0.04$) as we had no *a priori* reason to expect a delayed response.

Population flux across removal boundary

The net effects of home-range movements on the distribution of the population are well-summarised by the local population flux across successive north–south lines parallel to the removal boundary (Fig. 4). We measured the flux as the number of home-range displacement vectors crossing a parallel from east to west minus the number crossing from west to east. The westward flux in the first year post-removal peaked just inside the removal boundary and vanished beyond 200 m. At the boundary there was a net flux of 19 possums west across 277 m of boundary. There was little or no net flux in the second year.

The mean penetration into the removal area of westward-moving possums was 44 ± 6.9 m ($n = 21$, range 2–116 m), or

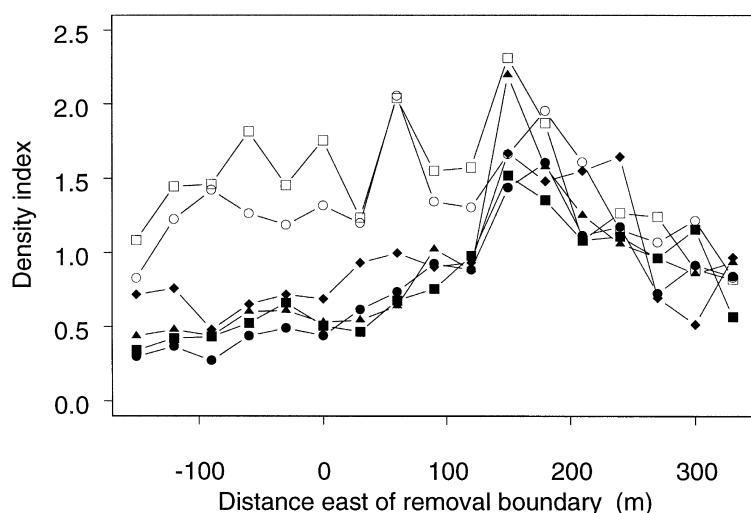


Fig. 3. Profile of possum density across the trapping grid before and after the removal of 80% of animals from one end. The density index was constructed from trap success by the method of Linn and Downton (1975). Each curve is the averaged estimate for 12 nights in 3 trapping sessions. Pre-removal: ○–○ September 1993 to February 1994; □–□ April 1994 to August 1994. Post-removal: ●–● October 1994 to February 1995; ■–■ April 1995 to August 1995; Δ–Δ October 1995 to February 1996; ◆–◆ April 1996 to August 1996. Density in the removal area had not fully recovered after 2 years. The number of traps per line declined from left (11) to right (5) and the variance of the index increases correspondingly.

Table 3. Distribution and survival of resident brushtail possums and new recruits between an area of lowered density (the 'removal area') and an equal adjacent area of forest at 1 and 2 years after density reduction

Trap-revealed range centres. Survivors either remained *in situ* or transferred to the opposite block

Sample	Enumerated population	
	Removal area	Non-removal area
Initial population (Aug 1994)	106	102
Killed	70	0
Post-removal Year 1 (Aug 1995)		
Surviving <i>in situ</i>	9	71
Surviving, moved	23	1
New, native-born	3	10
New, unknown	6	6
Post-removal Year 2 (Aug 1996)		
Surviving <i>in situ</i>	26	61
Surviving, moved	5	3
New, native-born	8	14
New, unknown	12	3

48 ± 8.3 m ($n = 14$, range 11–116 m) if the sample is restricted to movements that were significant by the MRPP test. The mean for females (48 ± 10.3 m, $n = 12$) did not differ significantly from that for males (37 ± 8.6 m, $n = 9$).

Individual behaviour in response to density gradient

Range shifts by surviving residents (Fig. 5) contributed to the smoothing of the experimentally induced density gradient. Range shifts tended to be oriented towards the removal area in the first year post-removal (angular mean 268° , angular deviation 106° ; $P = 0.008$), but not in the second year (angular mean 18° , angular deviation 116° ; $P > 0.25$).

MRPP tests detected significant changes in the distribution of captures ($P < 0.05$) for 35% of 93 surviving residents

between the pre-removal period and the first year post-removal, and for 14% of 88 survivors between the first and second years post-removal. Data were inadequate to test 11 animals in the first interval and 8 animals in the second interval. The trap-based index of home-range size did not change significantly between the pre-removal period and the first year post-removal in either sex (females: 33.6 ± 2.7 m v. 32.9 ± 2.3 m, $P = 0.16$; males: 45.2 ± 3.5 m v. 41.9 ± 2.2 m, $P = 0.63$). The significant MRPP test statistics therefore probably represented changes in the location rather than the size of home ranges.

Trap-revealed displacements between the pre-removal period and the first year post-removal averaged 22.5 ± 6.6 m towards the removal area ($n = 91$, range 238 m to -120 m). This figure increased to 45.3 ± 16.6 among animals showing a change in home range by the MRPP test ($P < 0.05$). The distance moved to the west did not vary significantly with distance from the removal area or between the sexes ($P > 0.50$) for the MRPP sample.

Initial location versus probability of moving

Observed percentages of possums moving >50 m to the west were 29% in the zone 0–100 m outside the removal boundary ($n = 38$), 25% at 101–200 m ($n = 28$), and 4% at >200 m ($n = 28$). Although sex was not on its own a strong predictor of the probability of moving ($P = 0.6$), it was found to interact strongly with distance in logistic regression models ($P = 0.01$). Separate models were therefore fitted for males and females. Distance from the removal area was a highly significant effect in both sexes (Table 4). Among females the predicted probability of moving declined monotonically away from the removal area (Fig. 6a). Among males the fit was improved by including a quadratic term in easting and the predicted probability of moving peaked about 125 m outside the removal boundary (Fig. 6b).

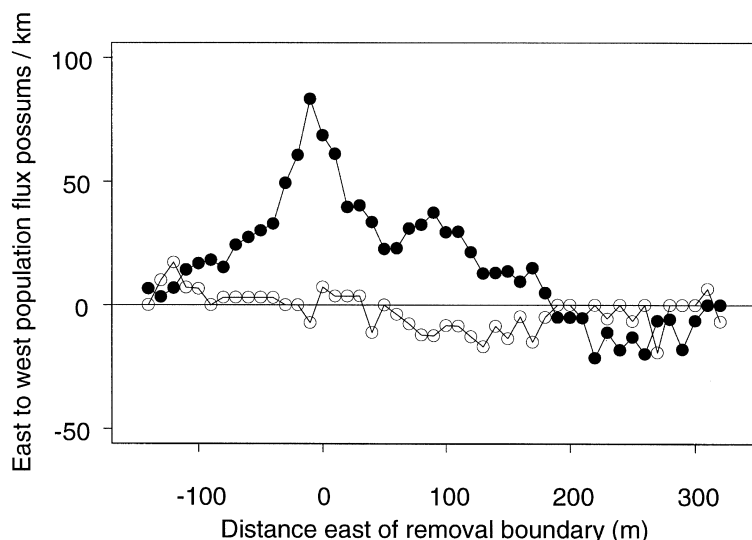


Fig. 4. Spatial flux one year and two years after partial control of the brushtail possum population at the study area. Net spatial flux (the number of trap-revealed home-range displacement vectors crossing from east to west minus the number crossing from west to east) is plotted for north-south transects at successive 10-m increments of distance from the boundary. ●–● pre-removal (April 1993 to August 1994) to Post-removal Year 1 (December 1994 to October 1995); ○–○ Post-removal Year 1 (December 1994 to October 1995) to Post-removal Year 2 (December 1995 to October 1996).

Other characteristics of movers

No interaction terms were included in the single-sex models by the selection algorithm in the stepwise model and it is therefore only necessary to consider main effects. Initial maturity and average body weight both improved model fit by the AIC criterion for females, but not for males (Table 4). Immature females tended to move less than mature females, but light females (<2000 g) were more likely to move than heavier ones. Neither of these effects appeared significant when its associated deviance was compared with a Chi-squared distribution, and their biological significance remains in doubt.

Inclusion of range size as a predictor significantly improved the fit of the logistic regression model for males but not for females (Table 4). The effect appeared to be non-linear: the probability of moving was much greater for males with large ranges.

Radio-telemetry

There was a highly significant linear relationship between the trap-revealed and radio-revealed east–west displacements in the first year post-removal ($R^2 = 0.27$, $P = 0.009$). The intercept did not differ significantly from zero and the slope did not differ from 1.0, suggesting that trapping data were an adequate, if noisy, measure of location. Radio-tracked animals from the 100-m zone adjacent to the removal area shifted their radio centre on average 28 ± 7.7 m towards the removal area in the first year ($n = 19$, range –20 to 119 m), and 22% shifted at least 50 m.

Although telemetry data were collected for relatively few animals they provided unique insights into the timing of range shifts and changes in the structure of home ranges. Contour plots of activity showed that 9 animals (all females) had stable bimodal activity distributions in the pre-removal period, in each case comprising one mode within the removal area and one to the east, separated by 100–200 m of little-

used forest. These individuals all had large trap-revealed ranges (mean deviation >40 m). The reason for these irregular range structures is unknown. After the removal, 7 animals with initially bimodal ranges remained bimodal and 2 concentrated their activity on a single mode within the removal area. A single female showed a trimodal range straddling the removal boundary both before and after removal. Two possums with initially unimodal ranges outside the removal area established a second mode within the removal area. Range shifts were incremental in the sense that the new range included a large part ($\geq 50\%$) of the previous range.

The detailed timing of shifts was examined for four animals whose mapped radio ranges clearly changed in the year following the removal (Fig. 7). In each case a change in the distribution of radio-fixes was apparent by the tracking session in October 1994, immediately after the removal period (Fig. 8).

Discussion

Understanding the spatial dynamics of possum populations and the responses of individual possums to neighbour removal is essential if cost-effective control strategies are to be developed. If adjoining landowners do not cooperate effectively, control can become disjointed, both in time and space. Where one landowner imposes control and another does not, any resulting flux of possums across the boundary imposes an external cost on the owner of the controlled land (Bhat *et al.* 1993). Vacuum effects as we defined them are the most direct mechanism driving such a flux. It is desirable that they be incorporated in models of the spatial dynamics of pest populations in order to improve the accuracy of predictions and model-based pest-management strategies (e.g. Barlow 1993; Efford 1996).

This study provides the first decisive evidence for a vacuum effect in brushtail possums. In previous removal studies it has not been possible to identify the source of

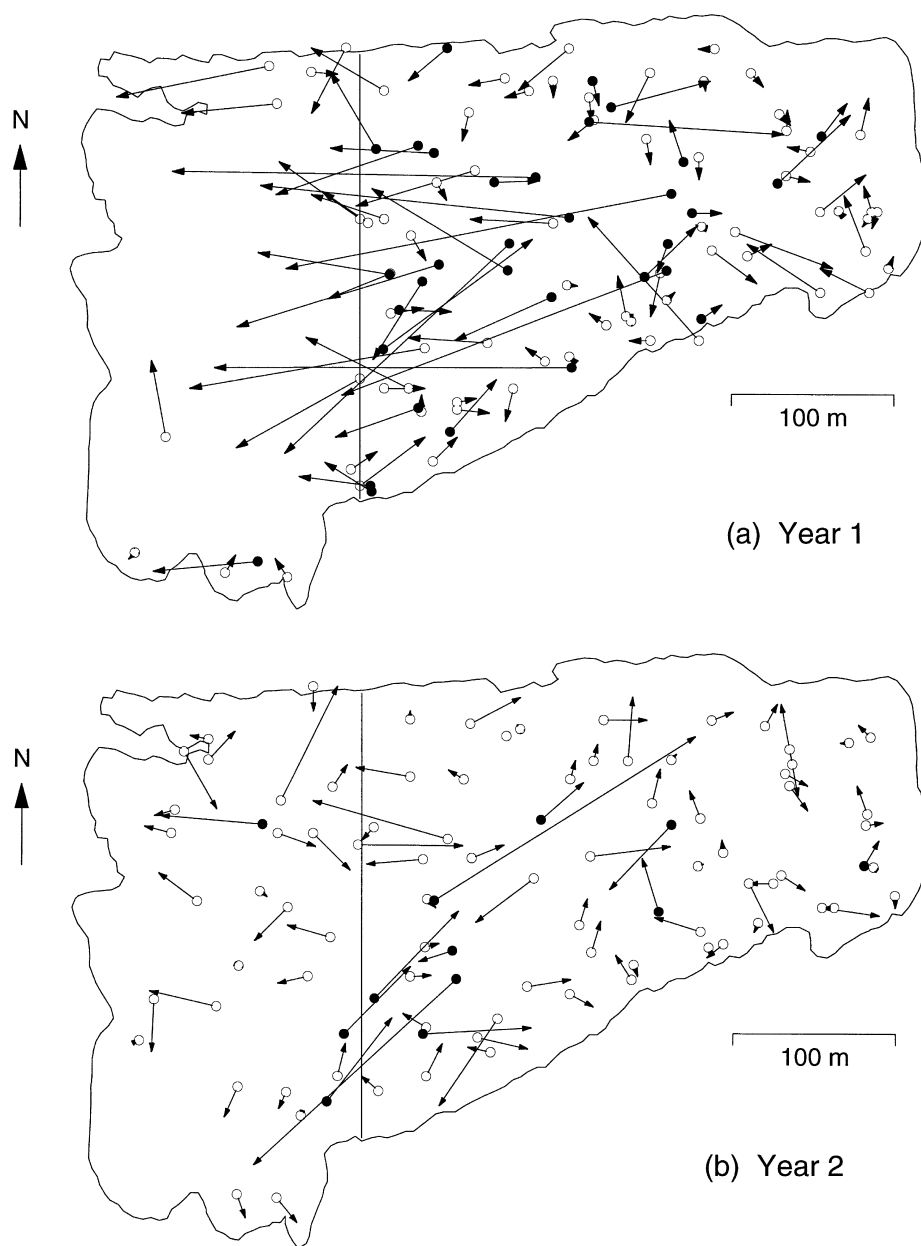


Fig. 5. Trap-revealed shift in range centres of brushtail possums exposed to an experimental density gradient at the study area. Arrows connect range centres in successive years; individuals were included only if they were known to be alive in August of both years. Circle at base of arrow is filled when MRPP also indicated a significant change in home range ($P \leq 0.05$). Vertical line marks nominal boundary of removal area. (a) Post-removal Year 1, 1994-95; (b) Post-removal Year 2, 1995-96.

immigrants or to eliminate the possibility that immigration of equal magnitude would have occurred without the removal (e.g. Green and Coleman 1984; Clout and Efford 1984).

The vacuum effect at Pigeon Flat was notable for its short range (<200 m). Our data confirm the strong site attachment of most possums. Radio-tracked female possums that shifted in response to our manipulation assumed new ranges that largely overlapped their previous range and completed the shift in a matter of weeks. Thereafter they were loyal to the new range. Clearly, some foraging and exploratory movements were made outside the 75% ranges we mapped, but we cannot reliably distinguish these from telemetry errors and they appear not to play a role in the vacuum effect. We spec-

ulate that the factors causing individual possums to shift probably operate within their core activity areas (e.g. within the 75% activity contour) rather than at the periphery of their range. This is consistent with the observed spatial scale. The abrupt timing of at least some shifts further leads us to the speculation that female movers responded to changes in their social environment (i.e. loss of immediate neighbours) rather than directly to increased *per capita* access to resources. We cannot, however, eliminate the possibility that movers benefited from increased foraging rates as a result of reduced interference.

Our data are inadequate to place an upper limit on the speed with which range adjustment occurs. It is possible that ranges change within days. We note that a rapid vacuum

Table 4. Individual predictors of probability of possum movement in response to control

Simplified logistic regression models derived by stepwise changes to an initial model including easting (distance from controlled area), sex, maturity, range size and average body weight as predictors. Analysis of deviance for the resulting model with terms fitted sequentially. Poly(Easting, 2) refers to a second-order orthogonal polynomial term in Easting. Main effects and second-order terms were dropped or added if this reduced Akaike's Information Criterion for the model as a whole. Although not significant on their own ($P < 0.05$), 'Maturity' and 'Body weight' were retained in the model for females as they reduced the AIC

Model	Change in		Residual		$P(\chi^2)$
	d.f.	Deviance	d.f.	Deviance	
Females					
Null model			55	49.37	
Easting	1	13.50	54	35.88	0.0002
Maturity	1	1.61	53	34.26	0.204
Body weight	1	3.64	52	30.62	0.056
Males					
Null model			30	35.40	
Poly(Easting, 2)	2	10.04	28	25.37	0.007
Range size	1	8.63	27	16.73	0.003

effect has the potential to bias trap-line methods for monitoring abundance. The rate of movement appeared to decline rapidly over time despite the persistence of a (reduced) density gradient. Nakata and Satoh (1994) also observed a rapid decline in the tendency of the gray red-backed vole, *Clethrionomys rufocanus bedfordiae*, to recolonise an area of low density, which they attributed to seasonal and demographic factors (low dispersal in winter and in declining populations). We can eliminate seasonal effects as there was no resurgence of movement in spring of the second year, but several alternatives remain. Movement may have been non-linear on the density gradient (ceasing as soon as the initial contrast had been 'smoothed off'), or the initial pulse of movement may have exhausted the pool of potential movers if these are a limited subset of surviving neighbours defined by some unknown criterion.

It was surprising that males near the edge of the removal area did not move while those further away did. We suggest that several apparent movements of males were due to a trapping artifact resulting from the steep gradient in trap saturation at 120–150 m from the removal boundary that persisted through the post-removal period. Unfortunately, we did not attach radio-transmitters to males in this zone so we are unable to test this interpretation directly. However, it is consistent with both the larger ranges of males than of females and the significant effect on movement probability of range-size differences among males but not among females. A sharp gradient in probability of capture will have a greater absolute effect on the apparent locations of animals with large ranges because such animals are more likely to overlap the gradient and because a given sampling bias translates into a larger displacement.

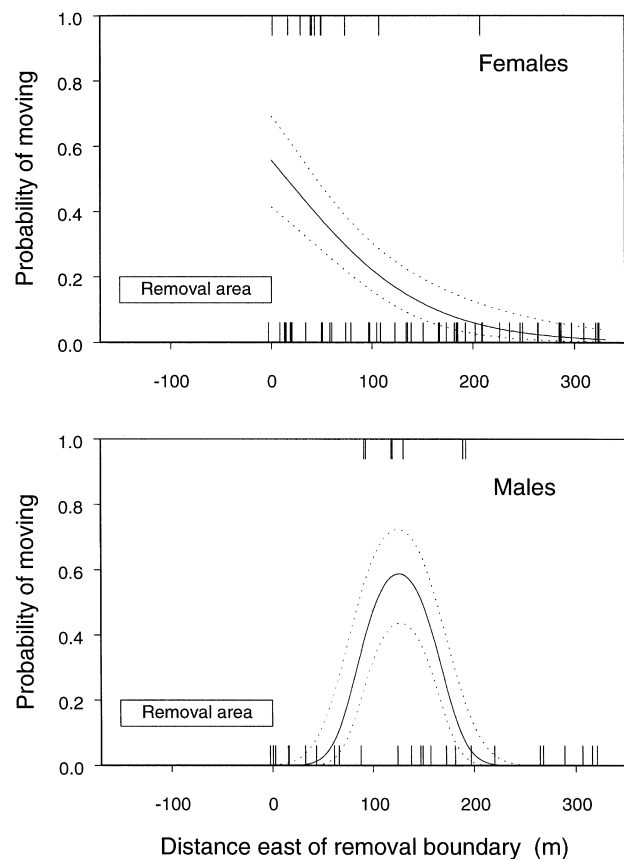


Fig. 6. Effect of distance from removal boundary on the predicted probability that a possum moved its trap-revealed range ≥ 50 m towards a removal area in the first year post-removal. Curves were predicted by the logistic regression models of Table 4; the effects of other predictors were held constant. (a) Females, (b) males. Tick marks within frame indicate initial location of possums that moved (upper) or did not move (lower). Dotted lines indicate pointwise ± 1 s.e. limits for the mean. The response of females was greatest near the nominal boundary of the removal area, whereas the response of males was greatest where the persistent density gradient was greatest (cf. Fig. 3).

The contribution of the vacuum effect to recolonisation after control will depend critically on scale and proximity to uncontrolled areas. The 'vacuum effect' flux across the removal boundary in the first year replaced only 19 of 70 (27%) of the animals removed. Many circumstances of this study favoured a large vacuum effect (small removal area, steep density gradient and many ranges overlapping boundary). However, a greater replacement rate would be expected if the same removal were to be applied to a similar-sized patch within continuous forest. Replacement might then be completed within one year for a patch with four times as much edge and the same area ($4 \times 27\% > 100\%$). This simple linear arithmetic is unlikely to hold as the influx would presumably diminish as density approached carrying capacity. However, it is interesting (and safer) to consider how an edge effect of the magnitude we measured would extrapolate to the larger scale of Barlow's

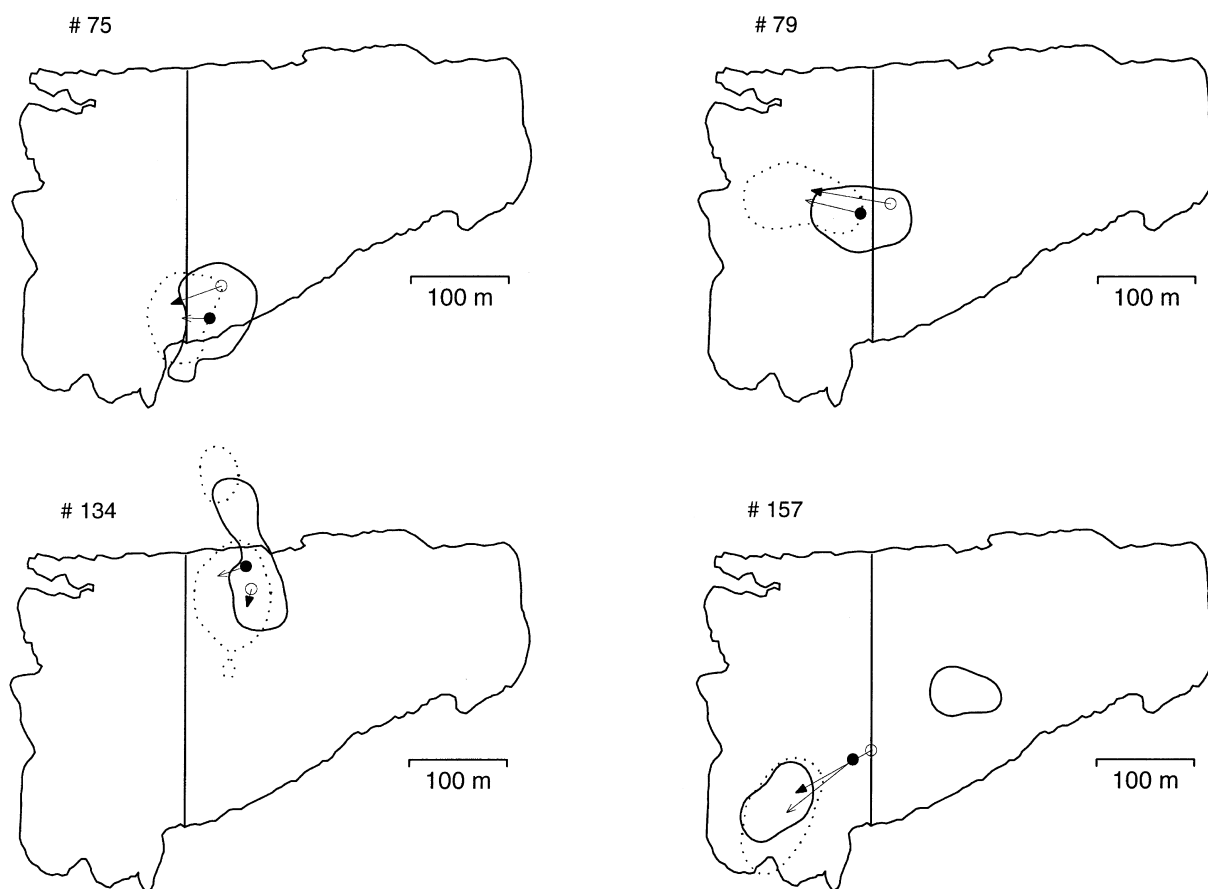


Fig. 7. Home-range shifts of selected brushtail possums in an induced density gradient at the study area. Contours enclose 75% of night-time radio fixes: solid line July 1993 to August 1994; dashed line December 1994 to October 1995. Vectors indicate shift of arithmetic range centre between pre-removal period and first year post-removal: solid, radio-revealed; open, trap-revealed. Vertical line marks the eastern boundary of the August–October 1994 removal area.

(1993) model for the spatial dynamics of brushtail possums. He speculated that a depopulated central 1-km grid square would receive an annual influx corresponding to 10% of the population differential between that square and each of the 8 adjacent squares. Substituting our population densities (3 ha^{-1} and 16 ha^{-1}), his model predicts a boundary flux of $0.1 \times (1600 - 300) \times 8$ or 1040 animals. If the flux we observed at the removal boundary (68.5 km^{-1}) applied along the 4-km edge of the central square then it would receive only 274 immigrants, or 26% of the number predicted under Barlow's model. More significantly, these animals would colonise only the outer fringe of the square, and negligible movement would be expected in subsequent years despite the persistence of a density contrast. We suggest that the vacuum effect would be more accurately modelled as a one-off response to a disturbance event rather than as a response to a density gradient.

The key to extrapolating our results to other sites appears to be home-range size and shape. Redistribution of foraging activity within a home range can result in a large apparent linear shift when the initial range is elongated in the direction of interest. Fortuitously, this was the case for many of our

bimodal ranges as they straddled the removal boundary. Comparable situations occur where possums routinely move long distances from within forest to feed on pasture (e.g. Green and Coleman 1986). We suggest that such a pre-existing pattern of range use may explain instances of rapid population recovery after control on forest/pasture margins. Conversely, when ranges are small or unimodal the vacuum effect will make a negligible contribution to recovery even on scales of 5–10 ha.

Long-distance natal dispersal in brushtail possums is biased towards young males (e.g. Clout and Efford 1984). If we are right that some apparent movements of males were an artifact of trap saturation, then relatively few males moved in response to the artificial density gradient itself. Our evidence would then indirectly support Green's (1984) contention that female brushtail possums and not males exhibit territoriality, in the sense of defending a core area of the home range. The existence of a vacuum effect among adult females is particularly significant as their numbers govern the rate of *in situ* recruitment in promiscuous or polygynous mating systems, such as probably apply to possums (e.g. Cowan 1990). The

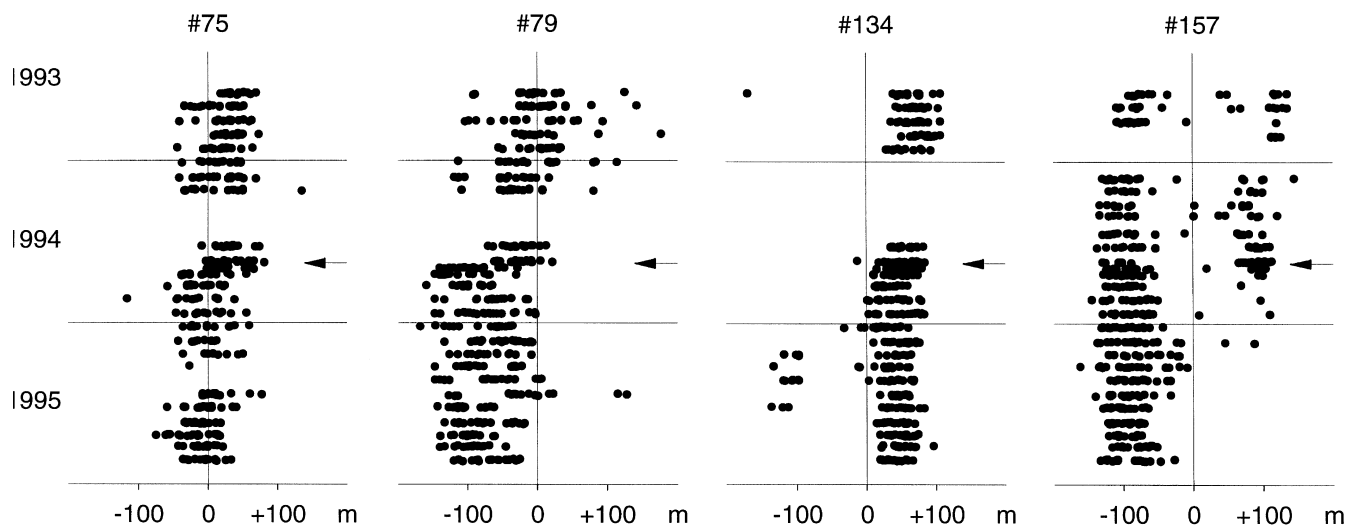


Fig. 8. Timing of home-range shifts of selected brushtail possums in relation to abrupt creation of a gradient in population density at the study area. Dots are east–west projections of night-time radio-fixes plotted against date (reversed vertical scale). Arrows mark initial removal of other animals with home-range centres to the west of zero on the *x*-axis in August 1994. Points were jittered slightly to enhance perception of density. Within a month of the start of removal, Animals 75, 79 and 134 shifted their unimodal ranges slightly to the west, and Animal 157 largely abandoned its previous activity mode outside the removal area.

initial settlement of females may also facilitate the settlement of males if, as we expect from theory, males settle to maximise their access to potential mates (e.g. Davies 1991).

Acknowledgments

We thank Mr Allan Brown and Ms Diane Caulfield, Mr Colin Baird and Mr Steve Smith for allowing us access over their respective properties and helping in many other ways. Ros Cole, Morgan Coleman, Steeve Côté, Kev Drew, Richard Heyward, Mark Müller, Monique Poulin and Grit Walther assisted in the field. Bill Lee and Ralph Allen described the vegetation. John Baldwin and Mark Peters assisted with surveying. Kevin Lay of Sirtrack Ltd helped us with the radio-telemetry system. Peter Bayliss, Peter Caley, and Phil Cowan made many useful comments on a draft. This work was funded by the New Zealand Foundation for Research, Science and Technology (C09301) and the New Zealand Animal Health Board (316/92).

References

- Barlow, N. D. (1993). A model for the spread of bovine Tb in New Zealand possum populations. *Journal of Applied Ecology* **30**, 156–164.
- Berry, K. J., and Mielke, P. W. Jr (1983). Computation of finite population parameters and approximate probability values for multi-response permutation procedures (MRPP). *Communications in Statistics* **12**, 83–107.
- Bhat, M. G., Huffaker, R. G., and Lenhardt, S. M. (1993). Controlling forest damage by dispersive beaver populations: centralised optimal management strategy. *Ecological Applications* **3**, 518–530.
- Boutin, S., Gilbert, B. S., Krebs, C. J., Sinclair, A. R. E., and Smith, J. N. M. (1985). The role of dispersal in the population dynamics of snowshoe hares. *Canadian Journal of Zoology* **63**, 106–115.
- Carothers, A. D. (1971). An examination of Leslie's test of equal catchability. *Biometrics* **27**, 615–630.
- Carothers, A. D. (1979). Quantifying unequal catchability and its effect on survival estimates in an actual population. *Journal of Animal Ecology* **48**, 863–869.
- Chambers, J. M., and Hastie, T. J. (Eds) (1993). 'Statistical Models in S.' (Chapman & Hall: New York.)
- Clout, M. N., and Efford, M. G. (1984). Sex differences in the dispersal and settlement of brushtail possums (*Trichosurus vulpecula*). *Journal of Animal Ecology* **53**, 737–749.
- Clout, M. N., and Gaze, P. D. (1984). Brushtail possums (*Trichosurus vulpecula* Kerr) in a New Zealand beech (*Nothofagus*) forest. *New Zealand Journal of Ecology* **7**, 147–155.
- Cowan, P. E. (1990). Family Phalangeridae. In 'The Handbook of New Zealand Mammals.' (Ed. C. M. King.) pp. 67–98. (Oxford University Press: Auckland.)
- Davies, N. B. (1991). Mating systems. In 'Behavioural Ecology'. 3rd Edn. (Eds J. R. Krebs and N. B. Davies.) pp. 263–294. (Blackwell: Oxford.)
- Dice, L. R., and Clark, P. J. (1953). The statistical concept of home range as applied to the recapture radius of the deer mouse (*Peromyscus*). Contributions from the Laboratory of Vertebrate Biology University of Michigan, No. 62 (15 pp.).
- Dueser, R. D., Rose, R. K., and Porter, J. H. (1984). Body-weight criterion to identify dispersing small mammals. *Journal of Mammalogy* **65**, 727–729.
- Efford, M. G. (1992). Revised estimates of the bias in 'minimum number alive'. *Canadian Journal of Zoology* **70**, 628–631.
- Efford, M. G. (1996). Simulating spatially distributed populations. In 'Frontiers of Population Ecology'. (Eds R. B. Floyd, A. W. Sheppard, and P. J. De Barro.) pp. 409–418. (CSIRO Publishing: Melbourne.)
- Efford, M. G. (1998). Demographic consequences of sex-biased dispersal in a population of brushtail possums. *Journal of Animal Ecology* **67**, 503–517.
- Green, W. Q. (1984). A review of ecological studies relevant to management of the common brushtail possum. In 'Possums and

- Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 483–499. (Surrey Beatty & Sons: Sydney.)
- Green, W. Q., and Coleman, J. D. (1984). Response of a brush-tailed possum population to intensive trapping. *New Zealand Journal of Zoology* **11**, 319–328.
- Green, W. Q., and Coleman, J. D. (1986). Movement of possums (*Trichosurus vulpecula*) between forest and pasture. *New Zealand Journal of Ecology* **9**, 57–69.
- Johnson, N. L., and Kotz, S. (1970). 'Continuous Univariate Distributions.' (John Wiley: New York.)
- Krohne, D. T., and Miner, M. S. (1985). Removal trapping studies of dispersal in *Peromyscus leucopus*. *Canadian Journal of Zoology* **63**, 71–75.
- Larsen, K. W., and Boutin, S. (1995). Exploring territory quality in the North American red squirrel through removal experiments. *Canadian Journal of Zoology* **73**, 1115–1122.
- Linn, I. J., and Downton, F. (1975). The analysis of data obtained from small mammal index trapping. *Acta Theriologica* **20**, 319–331.
- Nakata, K., and Satoh, K. (1994). Distance of movements of voles after removal in *Clethrionomys rufocanus bedfordiae* (Rodentia: Cricetidae). *Applied Entomology and Zoology* **29**, 97–103.
- Nichols, J. D., and Pollock, K. H. (1983). Estimation methodology in contemporary small mammal capture–recapture studies. *Journal of Mammalogy* **64**, 253–260.
- Pledger, S. A., and Efford, M. G. (1998). Correction of bias due to heterogeneous capture probability in capture–recapture studies of open populations. *Biometrics* **54**, 888–898.
- Schieck, J. O., and Millar, J. S. (1987). Can removal areas be used to assess dispersal of red-backed voles? *Canadian Journal of Zoology* **65**, 2575–2578.
- Seber, G. A. F. (1982). 'The Estimation of Animal Abundance.' 2nd Edn. (Charles Griffin & Co.: London.)
- Scott, D. W. (1985). Averaged shifted histograms: effective nonparametric density estimators in several dimensions. *Annals of Statistics* **80**, 348–354.
- Statistical Sciences (1995). 'S-PLUS User's Manual. Version 3.3 for Windows.' (Statistical Sciences Inc: Seattle.)
- Stickel, L. F. (1946). The source of mammals moving into a depopulated area. *Journal of Mammalogy* **35**, 1–15.
- Tinkle, D. W., and Woodward, D. W. (1967). Relative movements of lizards in natural populations as determined from recapture radii. *Ecology* **48**, 166–168.
- Thomas, M. D. (1982). A radio-telemetry system for animal tracking in New Zealand. *New Zealand Journal of Science* **25**, 245–252.
- Thomas, M. D., Warburton, B., and Coleman, J. D. (1984). Brush-tailed possum (*Trichosurus vulpecula*) movements about an erosion control planting of poplars. *New Zealand Journal of Zoology* **11**, 429–436.
- Thomas, M. D., Frampton, C. M., Briden, K. W., and Hunt, K. G. (1995). Evaluation of brodifacoum baits for maintenance control of possums in small forest reserves. In 'Proceedings of the 48th New Zealand Plant Protection Conference'. pp. 256–259.
- Van Vleck, D. B. (1968). Movements of *Microtus pennsylvanicus* in relation to depopulated area. *Journal of Mammalogy* **49**, 92–103.
- Verts, B. J., and Carraway, L. N. (1986). Replacement in a population of *Perognathus parvus* subjected to removal trapping. *Journal of Mammalogy* **49**, 92–103.
- Ward, G. D. (1978). Habitat use and home range of radio-tagged opossums *Trichosurus vulpecula* (Kerr) in New Zealand lowland forest. In 'The Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery.) pp. 267–287. (Smithsonian Institution Press: Washington, DC.)
- White, G. C., and Garrott, R. A. (1990). 'Analysis of Wildlife Radio-tracking Data.' (Academic Press: San Diego.)
- Zar, J. H. (1996). 'Biostatistical Analysis.' 3rd Edn. (Prentice Hall: Upper Saddle River, NJ.)

Manuscript received 3 February 1999; accepted 2 August 1999