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MOVEMENT OF POSSUMS (*TRICHOSURUS VULPECULA*) BETWEEN FOREST AND PASTURE IN WESTLAND, NEW ZEALAND: IMPLICATIONS FOR BOVINE TUBERCULOSIS TRANSMISSION

Summary: Over a 3-year period, 1183 brushtail possums *(Trichosurus vulpecula)* were live-trapped in 125 ha of mixed hardwood forest and adjacent pasture in Westland, and 50 were radio-tracked for up to 14 months. Foraging movements between forest and pasture were much longer than previously reported. Twenty-eight percent of males and 18% of females denning c. 1000 m into forest were trapped on pasture at least once a year. These values were higher for possums denning closer to pasture, but dropped abruptly at distances beyond 1000 m and ceased beyond 1300 m into forest. Radio-tracking confirmed the trapping results and showed that possums travelled to and from pasture within the same night.

Age had little influence on travel to pasture, but males were twice as likely to travel as females. Pasture travel peaked in summer and autumn, coinciding with maximum pasture growth. Possums usually travelled less than 300 m beyond the forest edge, but foraged occasionally to 1300 m.

Possums moved vertically rather than horizontally across steep terrain, thereby minimizing travel between different food sources in the vertically stratified forest. Forest residents travelling furthest were those with dens 600-1000 m into forest. Consequently, control of possums in Tb-problem areas will be required over forest at least 1 km in from forest-pasture margins. Changes in farm management that reduce possum-cattle interactions are also desirable.

Introduction

The common brushtail possum *(Trichosurus vulpecula),* introduced from Australia (Pracy, 1974), was found to be a vector and reservoir of bovine tuberculosis (Tb), *Mycobacterium bovis,* in 1967 (Ekdahl, Smith & Money, 1970). It was directly associated with high levels of Tb in beef and dairy herds on some farms bordering indigenous forest (Julian, 1981). In 1976, the prevalence of Tb in infected possum populations on forest-pasture boundaries ranged from 2% to 12% at 23 localities throughout New Zealand (Julian, 1981). Further local outbreaks of Tb have occurred despite government spending of over $NZ2.5 million on direct Tb/possum control during the 1970's (Coleman, 1981).

Effective possum control on forest/pasture boundaries requires information on the distances possums travel to pasture from within forest, the frequency of such visits, the distances possums travel across the pasture, and the contact between possums travelling to pasture and with more sedentary residents within the forest. We investigated these factors in an extensive area of indigenous forest adjoining improved pasture, a typical site for bovine Tb, unlike previous habitats where possum movement had been studied (Crawley, 1973; Ward, 1978; Jolly, 1976; Clout & Efford, 1984). A progress report on this study was published earlier (Green & Coleman, 1981).

Study Area

The study area was on the forested, north-facing slope of Mt Bryan O'Lynn (42°37 'S, 171 °43 'E) and adjacent pasture land on the western flank of the Southern Alps. The area was laterally bounded by two prominent ridges about 600 m apart, and extended 2.5 km from pasture at 250 m altitude to the alpine shrubland limit at 1200 m (Fig. 1). The most important feature of the Mt Bryan O'Lynn forest was the broad altitudinal stratification (Coleman, Gillman & Green, 1980).

We divided the study area into eight 'home zones' for analysis of possum movements (see Methods); each zone covered a 100m vertical interval. Zone 1 included pasture and cutover *Weinmannia racemosa* forest between 200-300 m; zones 2 and 3 were dominated by *W. racemosa, Quintinia acutifolia* and tree ferns *(Cyathea smithii* and *Dicksonia squarrosa);* zones 4 to 6 included ridges dominated by *Metrosideros umbellata, W. racemosa,* and *Griselinia littoralis* associations; and the two high-altitude zones 7 and 8 were diverse habitats of cedar forests *(Libocedrus bidwillii)* grading to shrublands.

The climate was dominated by high rainfall and humidity. Rainfall at pasture level in 1976 and 1977 was 3242 and 2634 mm respectively, with no clear seasonal pattern. Mean daily temperature was 13-14°C in summer (December-February) and 4-6°C in winter

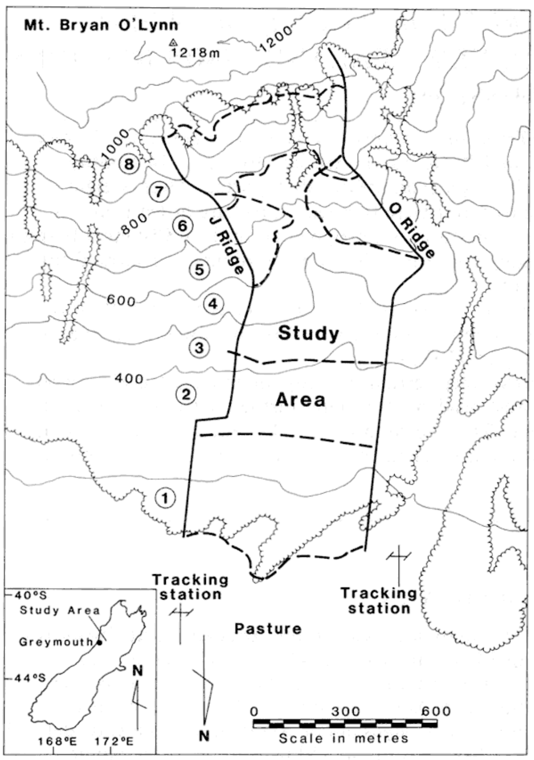

Figure 1: *Study area on Mt Bryan O'Lynn, Westland, New Zealand. The seven trap lines are shown as broken lines. Circles numerals* 1-8 *indicate home zones (see text).*

(June-August).

The livestock on the farmland were free of Tb and no infected possums were captured during the study.

Methods

Live-trapping and handling

Seven trap lines 300-400 m apart, each with 30-35 wire-mesh box traps, intercepted possums travelling to and from the pasture (Fig. 1). An additional 10-20 traps were set in varying locations on the pasture, up to 500 m from the forest. A total of 240 traps, baited and lured with apple, were set for three fine nights every month for 33 months (September 1975 - May 1978). Non-kill (knotted) snares were used briefly in zone 1, but proved too time consuming; 177 captures in snares were analysed as 'live-trap' records.

Possums were anaesthetised only at first capture; experienced handlers subsequently examined them without artificial constraints. Anaesthetic ether vapour was used, and only two animals (both in poor condition) died out of 1183 possums treated. Possums were marked with individual metal ear tags and ear tattoos. Capture sites were recorded.

Radio-tracking

Radio-tracking was also used to monitor movements and pasture utilization. Seventy-four possums were fitted with transmitters (Thomas, 1982), 70% from the low- to mid-altitude forests (zones 1-4), the remainder from mid- to high-altitude forests (zones 5-8). The locations of possums were determined by triangulation from two fixed tracking stations at the base of the hill (Fig. 1), operated on 5 nights per month for 14 months (April 1977 - May 1978). The operators were in radio contact, and 30-40 pairs of bearings were recorded per hour from sunset until dawn, in three shifts. The time calibration for location-fixes was based on elapsed time after official sunset. Since possums are nocturnal, their dens were located by day using a receiver with a hand-held, three-element yagi antenna.

Extinction trapping and aging

Almost all possums in the study area and two lateral buffer zones were killed by trapping during June and July, 1978 (Coleman *et al.,* 1980). All heads were collected and the lower second and third molars were extracted for aging by counting cementum annuli (Clout, 1982). Errors in aging were few: of 42 known-aged animals, 33 (79%) were correctly aged, and the remainder to ±1 year. Forty-three of the 50 radio-tracked possums used in analysis (see below) and most of the study population were aged.

Data analysis

Since the den sites of most possums were unknown, trapped possums were assigned to specific regions or 'home zones' (the zone in which they were captured most often) in order to calculate foraging ranges. Possums trapped equally in two zones were assigned to the zone more distant from the forest edge. A few individuals were assigned two, or very occasionally three, home zones when retrapping showed large, stable shifts over the years of the study. The movements of possums with three or more captures were analysed.

Radio-tracking spanned four complete seasons (autumn = March-May, winter = June-August, spring = September-November, summer = December-February) and a truncated autumn in 1977 (April-May). Since 60-100 radio-fixes were required to stabilize range areas (W.Q. Green & J.D. Coleman, unpublished.), only 28 males and 22 females (each with over 100 radio fixes), were included in the analysis of movement.

The accuracy of radio-fixes was assessed by comparing maps of animals trapped and 'fixed' over the same period. Six of the 50 radio-tracked possums captured less than five times were excluded from this comparison. Home range maps were drawn (Harvey & Barbour, 1965) using half the range length to determine the range perimeter after the outermost 5% of radio-fixes had been deleted by visual inspection. Factors influencing the frequency of pasture travel were tested for statistical significance using Duncan's Multiple Range Test (Steel & Torrie, 1980).

Results

Trapping and tracking success

Between September 1975 and May 1978, 1183 possums were live-trapped 9741 times. The sex ratio of 719 males to 464 females was significantly biased towards males (p<0.001). Extinction trapping in June-July 1978 yielded 773 females and 783 males, so it seems that males are more susceptible to live-trapping than females (Coleman & Green, 1984).

Over 14,700 radio-fixes were recorded for the 50 radio-tracked possums; the mean number per possum was 294 (range 100-620) over a 9-month period (range 3-14 months). These 50 possums were also tracked to dens 546 times (mean = 10.9) and were live-trapped an average of 20.2 times.

Comparison of trapping and radio-tracking methods

Trapping records were used to test whether radio tracked possums were a representative sub-set of the larger population. The frequency of pasture visits estimated from live-trapping for the 35 radio-tracked possums resident in zones 2-8, was compared with frequencies for 'trapped only' possums (232) with to or more trapping records (Table 1); no significant differences were evident for males (p = 0.4) or for females (p = 0.2).

There was good agreement between the areas occupied by possums based on radio-tracking and their known sites of capture. Only four of the 557 capture sites for the 25 males were outside the home range perimeters on the radio-tracking maps (by 60-210 m) and none of the 437 capture sites of the 19 females. In addition, known den sites were surrounded by many radio-fixes, which helped to confirm the accuracy of radio-tracking. There was no evidence of changes in movement patterns after transmitters were fitted.

Radio-tracking results were used to test for bias in the assignment of zones solely from trapping. The 50 radio-tracked possums were assigned zones from trapping data alone, then these estimated zones were compared with the known sites of their dens. Forty-six possums were correctly assigned from trapping data to the zone of their dens. Three of the remaining four

Table 1*: Comparison of pasture visits by radio-tracked and non-radio-tracked possums from live-trapping (% in brackets). The 'trapped only' animals were caught 10 or more times; the radio-tracked animals had five or more captures and 100+ radio-fixes. Zone 1 animals are omitted as zone traps were mostly on pasture.*

	Zones 2-4			Zones 5-8		
	Number visiting pasture	Not visiting pasture	N	Number visiting pasture	Not visiting pasture	N
A) Males						
Trapped and Radio-tracked	12 (80)	3	15	0	5	5
Trapped only	63 (72)	25	88	0	49	49
B) Females						
Trapped and Radio-tracked	3 (33)	6	9	0	6	6
Trapped only	22 (39)	34	56	0	39	39

possums were mismatched by one zone; all four were captured less than 10 times.

The comparisons of the techniques indicated that the radio-tracked possums were a representative sub-set of the trapped population, and that most 'trapped only' animals were correctly assigned to a zone.

Frequency of travel to pasture

The longest straight-line distance possums travelled from forest to pasture was between 1000 m (zone 4) and 1300 m (zone 5/6). Possums from more distant zones were neither trapped nor tracked on pasture. The frequency of travel to pasture decreased with increasing distance between the home zone and pasture, as shown by both trapping and radio-tracking (Table 2, Fig. 2). This decrease was abrupt; about 16% of the captures of zone 2 residents were on pasture, although the mean distance of the zone from pasture was only 400 m. The decrease in the frequency of pasture captures from zones 1 to 4 was significant for males ($F_{1,3}$ = 709, P <0.001) and females ($F_{1,3}$ = 988, p < 0.001) although the decreases between zones 3 and 4 were not significant (Table 2). From zones 5/6, pasture captures were only 0.5% of all male captures and 0.3% of all female captures and were excluded from the analysis.

Possums from zone 1 were excluded from estimates of the influence of season, age, and sex on pasture travel. Because traps in zone I were mostly on pasture, capture rates for zone I residents varied little and the high values 'swamped' those from other zones. Males travelled to pasture as often in summer as in autumn, and almost twice as often then as in winter and spring. Consequently, the overall variability between seasons was significant for males ($F_{1,3}$ = 6.1, p <0.001). Seasonal differences in pasture use by radio-tracked males were less pronounced than trap-revealed differences. Comparisons of the slopes of the regression equations (Fig. 2) indicated more pasture use by males in summer than in winter, but differences between other seasons were not strong. Females were twice as likely to travel to pasture in summer than any other season (Table 2) and the overall variability between seasons was significant (F $F_{1,3}$ = 3.6, p<0.05).

The frequency of captures on pasture was not influenced by the age of males (F $F_{1,3}$ = 1.0, P = 0.35) or of females (F $F_{1,3}$ = 1.5, P = 0.23). Males from zones 2-4 were twice as likely to travel to pasture as females. This applied to the trapped population as a whole (Table 2) and to radio-tracked possums in all seasons (Table 3). Males also spent significantly more time on pasture than females, since 36% of radio-fixes for males (total fixes = 6494) were on pasture

Table 2*: Influence of zone, season, age and sex on the frequency of captures on pasture. Means (%) ±95% confidence interval for each factor, using the 3 trapping years as replicates, are given. Result of Duncan's Test are shown as horizontal lines where joined means are not significantly different.*

Factor				
Zone	1	2	3	4
(zone-pasture distance in m)	(0)	(400)	(700)	(1000)
Male	94.6 ±4.4	22.7 ±5.4	9.8 ±4.7	7.2 ±5.0
Female	96.2 ±4.1	11.2 ±5.1	5.6 ±4.0	2.6 ±4.4
Season (*zones* 2-4)	Summer	Autumn	Winter	Spring
Male	17.7 ± 7.0	16.6 ±5.7	10.3 ±4.0	8.3 ±6.0
Female	11.0 ±6.7	5.6 ±5.4	3.4 ±3.2	5.9 ±4.4
Age (*zones* 2-4)	1 year	2-3 years	4 + years	
Male	14.5±8.8	13.8 ±6.8	11.3 ± 5.3	
Female	7.5 ± 7.9	7.5 ±4.4	4.5 ±6.2	
Sex (*zones* 2-4)	Male	Female		
	12.7 ±4.6	6.2 ±5.4		

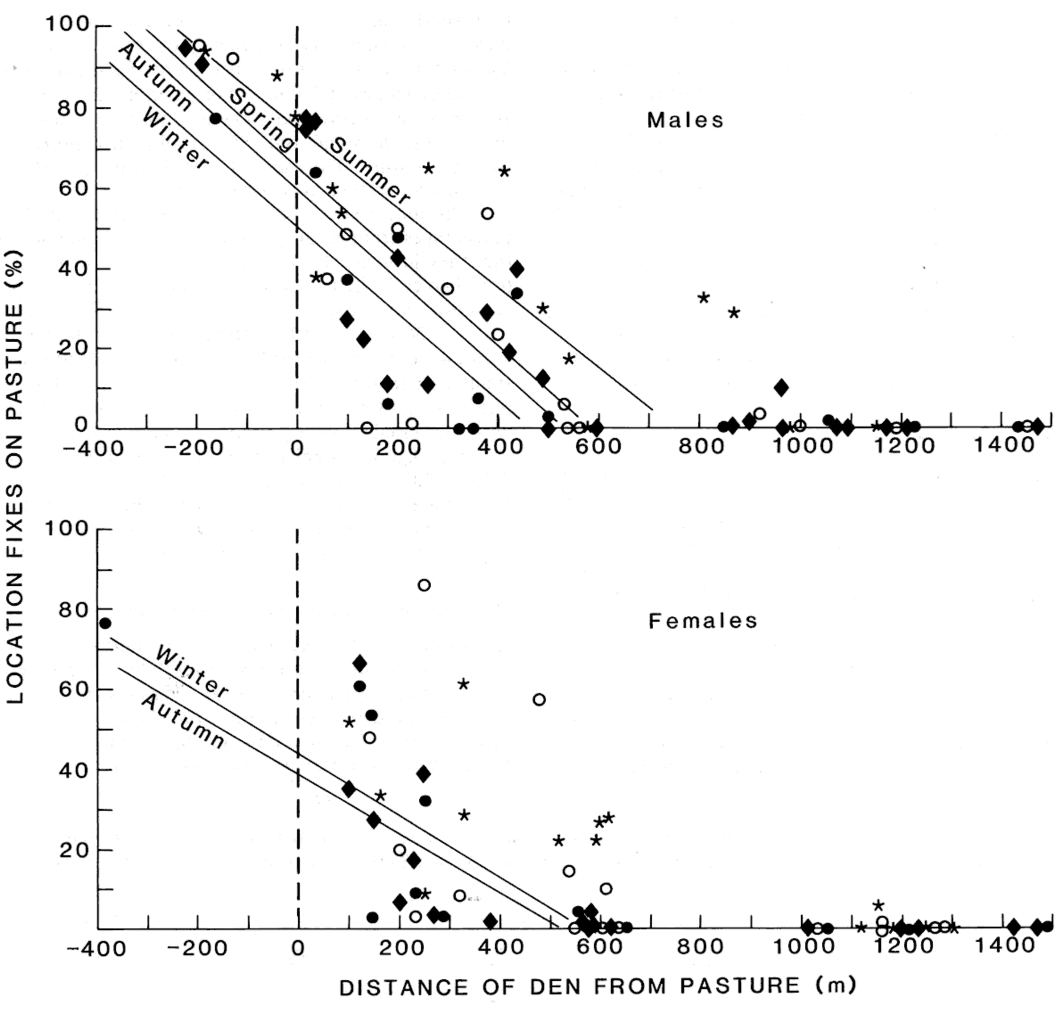

Figure 2: *Percentage of location-fixes on pasture as a function of den-to-pasture distance. Each datum point is the seasonal mean (spring o, summer *, autumn ♦, winter ●) of a radio-tracked possum derived from an average of 103 fixes/season for males and 110 for females. The vertical dashed line indicates the pasture-forest margin. Possums denning in trees and shrubs on pasture were assigned negative den-pasture distances. The best least squares straight line fit was obtained by regression and weighted according to the number of radio-locations/animal/season. Equations and r^2 values (in brackets) are based on data sets truncated at 700 m. MALES: spring y = 64.9 - 0.112x (.62), summer y = 75.5 - 0.100x (.76), autumn y = 60.2 - 0.112x (.76), winter y = 50.1 - 0.108x (.78). FEMALES: spring y = 35.0 - 0.030x (.05), summer y = 38.6 - 0.026x (.13), autumn y = 37.7 -0.71x (.54), winter y = 43.8 - 0.077x (.69).*

compared with 19.7% (n = 5336) for females (X^2 = 381.4, p<0.001).

Radio-tracking also revealed that the probability of residents in zones 2-4 travelling to pasture was highest in summer and lowest in autumn, for both sexes (Table 3). Testing these results against the hypothesis that pasture travel should be equally likely in all seasons showed significant variations for females (X^2 = 91.3, 3 d.f., p< 0.001), but not for males (X^2 = 5.8, 3 d.f., N.S.).

Overall, distance was the primary determinant of how frequently possums travelled to pasture, with its likelihood approaching zero at 1300 m into forest. Sex and seasonal effects were also significant; males were twice as likely as females to travel to pasture, females travelled most often in summer and males travelled most in both summer and autumn.

Pasture travel by home zone populations

While the frequency of travel to pasture will affect the probability of possums becoming infected with Tb, the probability of disease being transferred during each possum-stock interaction is also important. If disease transfer were highly likely, i.e., a single interaction would lead to infection, then the simple 'pasture visit -no pasture visit' status of possums would be more relevant than the number (frequency) of visits.

We calculated the 'visit - no visit' status by zone as the percentage of the population in each zone that was trapped on pasture at least once a year (Table 4). As these values depended on the time interval over which they were measured, seasonal values were less than yearly values. Zone 1 was again excluded for most comparisons (see 'Frequency of travel...'). Values for zones 2-4 were much higher than equivalent frequency values in Table 2. For example, 23% of the zone 4 possums travelled 1000 m to pasture at least once a year, although only 5% of all their captures were on pasture. Thus some forest-dwelling possums travelled to pasture only occasionally.

Distance, season, sex, and age influenced the percentages trapped on pasture in the same manner that they influenced the frequency of travel to pasture (c.f. Tables 2, 4). Distance was again the major factor for both sexes (males: $F_{1,3}$ = 78.5, p<0.001; females $F_{1,3}$ = 36.2, p< 0.001), although values from zones 3 and 4 were similar (Table 4). Season was almost a significant factor for females ($F_{1,3}$ = 2.4, p = 0.07), and was significant for males ($F_{1,3}$ = 3.8, p< 0.05), with more males visiting pasture in summer and autumn. Age was significant only for females ($F_{1,3}$ = 4.4, p<0.05), with a smaller proportion of 4+ -year-old females trapped on pasture than younger females. During the average year, 44% more males than females in zones 2-4 travelled to pasture ($F_{1,3}$ = 4.6, p = 0.05).

Distribution of forest and pasture movements

Radio-tracking showed that possums ranged extensively through the forest from their home zone, as well as across pasture (Fig. 3). Possums from zones 3 and 4 moved furthest and not only ranged 600 + m across pasture, but also into sub-alpine regions. Zone 1 possums ranged the greatest distances across

Table 3: *Comparison of the frequency of travel to pasture by male and female radio-tracked possums. Data are from possums with dens in zones 2-4 (400-1000 m from pasture). Individual records have been summed for all animals within each sex and season class.*

	Spring		Summer		Autumn		Winter	
	♂	♀	♂	♀	♂	♀	♂	♀
No. nights with	<	>	<	>	<	>	<	>
Travel to pasture	43	65	34	26	37	11	43	20
No. nights without								
Travel to pasture	54	76	23	40	73	99	53	64
Total nights	97	76	57	66	110	110	96	84
χ^2 (1 d.f.)	17.630		5.029		18.014		8.669	
Significance	<0.001		<0.05		<0.001		<0.005	
Nightly probability of								
Travel to pasture	.44	.14	.60	.39	.34	.10	.45	.24

Table 4: *Influence of zone, season, age and sex on the percentage of populations caught on pasture at least once a year. Means (%) ± 95% confidence interval for each factor, using the 3 trapping years as replicates, are given. Results of Duncan's Test are shown as horizontal lines where joined means are not significantly different.*

Factor				
Zone	1	2	3	4
Male	98.3 ± 3.8	49.7 ± 7.0	24.3 ± 6.4	28.3 ± 22.1
Female	97.7 ± 4.6	37.7 ± 15.4	15.3 ± 12.2	17.7 ± 35.0
Season (zones 2-4)	Summer	Autumn	Spring	Winter
Male	29.2 ± 10.5	28.5 ± 9.5	16.8 ± 9.7	18.1 ± 7.0
Female	19.2 ± 9.5	11.3 ± 10.6	12.2 ± 9.8	7.3 ± 7.7
Age (zones 2-4)	1 year	2-3 years	4+ years	
Male	36.4 ± 14.4	34.1 ± 8.9	31.8 ± 10.2	
Female	33.0 ± 18.3	25.7 ± 7.4	12.1 ± 8.5	
Sex (zones 2-4)	Male	Female		
	34.1 ± 15.9	23.6 ± 26.5		

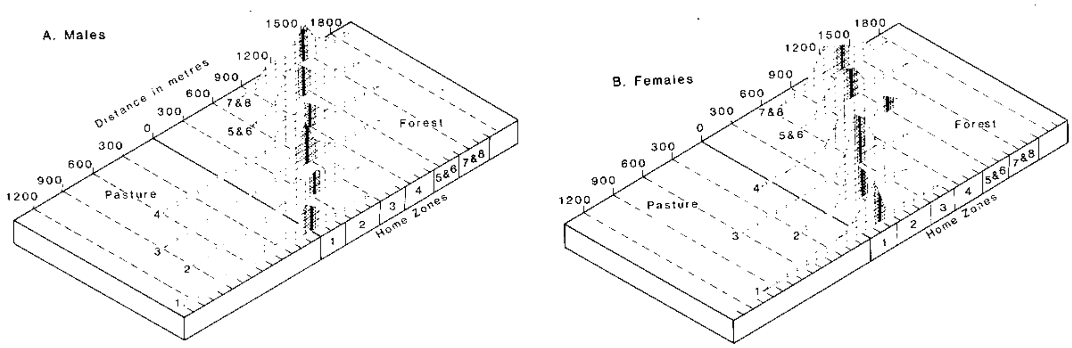

Figure 3: *Vertical distribution of location-fixes and den areas by zone for males and females. Heavy vertical lines and shading give mean locations of dens and* 95% *confidence intervals respectively. Vertical scale is marked in intervals of* 5%. *Sample sizes by zone (number of animals/number of location-fixes) are as follows: (a) Males: 1(7/2149);* 2 (8/2483); 3 (4/937); 4 (3/925); 5 + 6 *(4/660);* 7 + 8 (2/318). *(b) Females:* 1 (5/1742); 2 *(5/1710);* 3 (5/1283); 4 *(11602);* 5 + 6 (2/855); 7 + 8 (4/965).

pasture, with one male covering 1300 m. Thirty-seven percent of all radio-fixes of males on pasture were less than 2oo m from the forest edge and 57% of all fixes of females. A distance of 5oo m across pasture encompassed 51 % of the fixes of males and 87% of the females fixes. The difference showed the tendency of males to move further across pasture than females (Fig. 3).

Possums of both sexes and from all zones were at their maximum distance across pasture 3 hr 40 min. to 4 hr 20 min. after sunset. Mid-altitude possums travelled quickly to pasture and returned more slowly

(W.Q. Green and J.D. Coleman, unpublished), but on the same night.

Broad distribution patterns shown by radio-tracking and trapping were similar, although trapping gave a much coarser resolution of movements than did radio-tracking (Table 5). Most captures were made within the animal's home zone, and the wide spacing between trap lines contributed to this coarseness. Horizontal movements were much shorter than vertical movements. On average, radio-tracked possums ranged twice as far vertically as horizontally, and vertical movement was significantly greater for 44 of the 50 tracked possums (Table 6). Five of the remaining six possums also had larger vertical mean values, but large associated variances led to low F values. In zones 5-8, from which pasture travel was rare, travel over large vertical distances was less evident from trapping than from radio-tracking, although the absence of a trap line in alpine grassland meant that higher vertical travel would have passed unnoticed (Fig. 4).

Restricted horizontal movements were also revealed by measuring the interchange between residents of the two major ridges bounding the study area (Fig. 1). Only 11 % of all captures of residents on the ridges occurred in the central area, less than 300 m away, and less than 0.4% occurred on the opposite ridge (Table 7). Females from 'O' ridge were caught significantly less often off the ridge than male residents (X^2 = 12.7, p<0O.001). Similarly, females from the Centre area were caught less often on the ridges than were males (X^2 = 19.1, p<0.001) and

Table 5: *Distribution of captures between different zones. Values are the means (%) from 3 years of trapping.*

	Zone of capture (zone-pasture distance in m)						
A) Males							
Home Zone	1 (0)	2 (400)	3 (700)	4 (1000)	5/6 (1300)	7/8 (16000)	Captures (n)
1	94.1	4.9	0.3	0.0	0.2	0.5	885
2	21.3	75.9	2.8	0.0	0.0	0.0	816
3	9.2	8.7	80.5	1.3	0.0	0.3	589
4	8.0	3.7	5.3	78.1	4.7	0.2	512
5/6	0.4	0.1	0.3	6.9	86.5	5.8	727
7/8	0.0	0.0	0.0	0.3	7.3	92.4	354
B) Females							
1	96.0	2.4	0.9	0.0	0.3	0.3	328
2	11.6	87.1	1.3	0.0	0.0	0.0	527
3	4.3	2.2	91.3	0.8	1.0	0.4	491
4	2.4	2.4	2.8	81.9	10.5	0.0	248
5/6	0.2	0.0	0.0	2.8	90.3	6.7	506
7/8	0.0	0.0	0.0	0.0	4.3	95.7	302

Table 6: *Comparison of horizontal and vertical distances travelled nightly by radio-tracked possums. Males and females combined. Nightly values were calculated by measuring the horizontal and vertical displacement between the two outermost horizontal and vertical points. Nights with less than five co-ordinate pairs were omitted. This gave a mean of 27 nights/possum. Table values are means of the individuals' means by zone. Significance of difference was determined by F tests.*

Zone	Mean nightly distance (m) Horizontal	(± C.I.)	Vertical	(± C.I.)	Number of possums	Possums with larger Mean vertical Movements (p<0.05)
1	217	(± 48.6)	430	(±122.2)	12	9
2	194	(± 37.6)	375	(±122.1)	13	10
3	198	(± 42.1)	459	(± 119.1)	9	9
4	188	(± 25.4)	443	(±154.6)	4	4
5/6	160	(± 41.7)	328	(± 27.4)	6	6
7/8	160	(± 34.0)	374	(± 86.4)	6	6

females from 'J' ridge were caught less often off the ridge than were males ($X^2 = 4.9$, $p<0.05$). When three altitudinal strata (pasture + low forest, mid forest, alpine) were delineated, the same pattern of restricted horizontal movement was evident in all three strata.

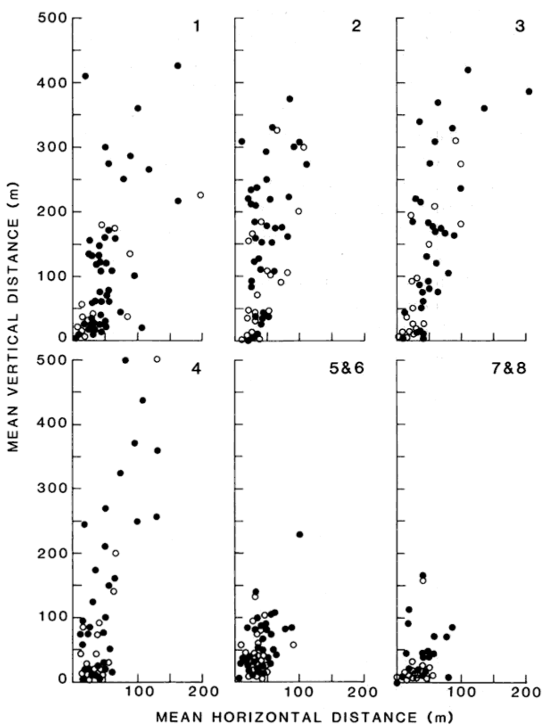

Figure 4: *Vertical and horizontal distances between successive capture locations. Mean values are plotted for all male (●)and female (○) possums with 10 or more captures. Numerals indicate home zones.*

Discussion

Comparison of movement patterns

Foraging movements by possums on low- to mid altitude slopes of Mt Bryan O'Lynn were much longer than has been reported from other populations. Details of home ranges will be reported in a later paper (W.Q. Green & J.D. Coleman, unpublished), but present results show that possums made nightly foraging movements of up to 1300 m between forest and pasture. Nearly 25% of possums resident 1000 m into forest travelled to feed on pasture at least once a year. Other New Zealand studies (see below) have reported range lengths of 300-350 m for males and 250 m for females, and average range lengths for brushtail possums in Australia are 390 m for males and 260 m for females (Green, 1984; Kerle, 1984).

The shorter range lengths from earlier studies in part reflect the limitations of trapping compared with radio-tracking (Ward, 1984). Yet even the shorter, trap-revealed movements from this study are at least twice those reported (Jolly, 1976; Ward, 1984; Thomas, Warburton & Coleman, 1984). Only ranges reported by Clout & Gaze (1984) (males = 530 m; females = 390 m) approach those of Mt Bryan O'Lynn possums.

New Zealand possum studies have covered a range of habitats; mixed hardwood forest (Crawley, 1973; Ward, 1978, 1984), *Nothofagus* forest (Clout & Gaze, 1984); and mixed shrubland-pasture (Jolly, 1976; Thomas *et al.*, 1984). However, none measured movements between improved pasture and adjoining areas of extensive indigenous forest. In other studies

Table 7*: Lateral movement within the study area shown by distribution of capture locations. Data from possums with 10+ captures, 1975-1978. Three 'residence areas' of roughly equal width were delineated ('J' ridge, Centre, '0' ridge - see Fig. 1), and possums were assigned to one as 'area of residence' based on capture locations.*

Area of residence	Number of captures (%) on: 'J' ridge	Centre	'O' ridge
A) Males			
'J' ridge	1049 (89)	126 (11)	3 (0)
Centre	89 (5)	1724 (89)	122 (6)
'0' ridge	9 (1)	160 (16)	801 (83)
B) Females			
'J' ridge	678 (92)	56 (8)	1 (0)
Centre	65 (5)	1292 (92)	42 (3)
'0' ridge	0	60 (11)	503 (89)

involving pasture and forest (Jolly, 1976; Thomas *et al.,* 1984), possums had to travel a few hundred metres, at most, to different habitats.

The strong vertical orientation of movements on Mt Bryan O'Lynn was induced by the vertical stratification of forest types and major food species on Mt Bryan O'Lynn (Coleman *et al.,* 1980; Coleman, Green & Polson, 1985). Possums encountered different foods more quickly by travelling vertically rather than horizontally. The predominance of vertical movements held in all zones, but was most marked where travel to pasture occurred (zones 1-4). Vertical stratification is a common feature of mixed hardwood forests in New Zealand. Only one other study has trapped possums over an altitudinal gradient (Clout & Gaze, 1984), and it revealed longer than average range lengths, perhaps as a consequence of the aItitudinally-stratified *Nothofagus* forest.

Possums are known to favour pasture species (Gilmore, 1967; Harvie, 1973; Warburton, 1978), and those on Mt Bryan O'Lynn were no exception. Pasture species comprised 120/0 of the yearly diet of possums denning within 300 m of the forest edge (Coleman *et al.,* 1985), and 90% of this was clover *(Trifolium* spp.) and grasses. Pasture foods were twice as common in male than in female diets in all zones, with a clear autumn peak for males. Consumption of pasture foods by females varied less between seasons, but doubled for residents of zones 3 and 4 in summer (J.D. Coleman & W.Q. Green, unpublished). These dietary patterns suggest a reason for possums travelling to pasture, and why males visited pasture more often than females. It is not known why pasture species should be differentially attractive to males. There was a discrepancy between the pasture feeding peak of males in autumn and the frequency of travel to pasture in both summer and autumn. Since males quickly lose condition during autumn breeding (Bamford, 1970), the discrepancy may indicate greater male activity associated with a change in feeding patterns at that time.

The higher use of pasture in summer and autumn coincided with the seasons of maximum pasture growth in this region. Radcliffe (1975a) measured pasture growth at Westport, 80 km away, which has similar climate and rainfall (2150 mm annual average). Pasture growth was highest in summer, when the yield of white clover *(T. repens)* also peaked. Perennial ryegrass *(Lolium perenne)* peaked in late summer/early autumn. However, where summer droughts are common, pasture growth peaks in spring (Radcliffe, 1975b). Use of pasture by possums in different parts of New Zealand may therefore vary with local patterns of pasture growth.

We assume that possums benefit nutritionally by feeding on pasture, although chemical analyses of the major forest species in possum diet are lacking. Fitzgerald (1976, 1978) showed that *Weinmannia racemosa* and *Metrosideros robusta* have low crude protein values of 5.5% and 5.7% respectively. White clover (24.6%) and grass regrowth (17.2%) have a higher crude protein content than any of the forest species measured by Fitzgerald (Lyttelton, 1973), which suggests higher protein levels could be one reason for pasture feeding. Possums trapped close to pasture were heavier than mid- to high-altitude possums (W.Q. Green & J.D. Coleman, unpublished), and population densities were highest at the pasture edge (Coleman *et al.,* 1980).

On Mt Bryan O'Lynn the proportion of the population travelling to pasture fell abruptly between zone 4 (1000 m from pasture) and zones 5/6, 1300 m from pasture. Presumably, an 'energetics boundary' lies between these zones beyond which the benefits of pasture feeding are outweighed by the calorific cost of getting there and back.

Defining the population 'at risk'

Since tuberculous lesions in possums typically contain huge numbers of bacteria and tuberculous animals can heavily contaminate pastures (Smith, 1972), pasture near a forest edge is the primary zone for Tb transmission as infection in possums is highest there (Cook & Coleman, 1975). Thus possums travelling to pasture are subject to a direct risk of infection, while those not travelling to pasture face an indirect risk through possible contact with infected animals within the forest. We assumed Tb transmission is more likely for possums facing direct risk, based on epidemiological evidence (J.D. Coleman, unpublished), although the relative extent of these risks has still to be evaluated.

A 'worst case' assessment of possums exposed to direct risk would include all possums that travelled to pasture at least once a year. The population thus at direct risk would include 98% of residents in zone 1, 38-50% (females, males) of residents in zone 2, and 17-26% (females, males) of residents in zones 3 and 4. Zones 1-4 covered over 50% of the study area, and contained about 70% of the possums (calculated from Coleman *et al.,* 1980).

If Tb transmission were more closely related to frequency of pasture use than to probability of a single visit, the population at direct risk would remain high in zone 1 (95%), but would drop by a factor of three in zones 2-4. Possums from higher zones (5-8), over 1300 m from pasture, were unlikely to be at direct risk because of their infrequent trips to pasture.

The population subject to indirect risk would effectively include all remaining possums on Mt Bryan O'Lynn because of the long vertical distances travelled and the extensive overlap of movements between home zones. As average possum density was 10.4/ha (Coleman, *et al,* 1980), the overlap of individual home ranges means most possums would be susceptible to indirect infection. Indirect transmission would also be possible to possums visiting pasture.

Implications for disease transmission and control

This study is relevant to the epidemiology and control of Tb in possum populations. Since forest residents make such long foraging movements, operations to reduce possum numbers in Tb-problem areas would need to encompass at least 1 km of forest adjacent to pasture. Only by controlling all possums at direct risk will the interaction between infected stock and possums be broken, presumably for long enough to 'decontaminate' pastures and herds before colonizing possums recommence feeding on pasture. A narrower control zone would still allow some possums to continue travelling to pasture. Where the problem is long-standing and the incidence of Tb in possums is high at the forest/pasture margin (> 10%), infection may already be present in the deep forest (Cook & Coleman, 1975), and control may be required further (1-2 km) into forest.

Further refinements in control practices will require better understanding of Tb epidemiology in possum populations. Corner and Presidente (1980, 1981) investigated laboratory transmission of Th, but little is known about transmission routes between possums in the wild, the rates and patterns of spread within populations, the role of density in sustaining Th reservoirs, the role of den sharing in Tb transmission, and movements of diseased possums. Why Tb should be so successful and persistent in some regions of New Zealand and not in others is unknown. Other wild animals (e.g., pigs, goats, and red deer) play an unknown role as Tb vectors and potential reservoirs.

Changes in farm management practices could help Tb control by lowering the likelihood of possum-cattle interactions. Beef and dairy herds should be kept out of forest where possum densities are high and Tb transmission is likely. Since possums forage most often on pasture within 200-300 m of forest, it would be preferable to graze sheep in this 'buffer zone' since they are more resistent to Tb (Zuckerman, 1980). This would be most effective in summer and autumn when possums use pasture most often.

The interaction of Tb and possums in New Zealand has obvious parallels to Tb in the badger *Meles meles* in south-west England (Zuckerman, 1980). The original transmission of Tb between possums or badgers and cattle probably took place on pasture. Intensive studies of the movement of badgers (Cheeseman *et al.,* 1981) and possums are now complete. Their contribution to a reduction in Tb levels in cattle herds will depend on the willingness and ability of management agencies to incorporate these findings into control practices.

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