Ecology of brushtail possums in a New Zealand dryland ecosystem

Alistair S. Glen*, Andrea E. Byrom, Roger P. Pech, Jennyffer Cruz, Astrid Schwab, Peter J. Sweetapple, Ivor Yockney, Graham Nugent, Morgan Coleman and Jackie Whitford

Landcare Research, PO Box 40, Lincoln 7640, New Zealand
*Author for correspondence (Email: glena@landcareresearch.co.nz)

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Abstract: The introduced brushtail possum (*Trichosurus vulpecula*) is a major environmental and agricultural pest in New Zealand but little information is available on the ecology of possums in drylands, which cover c. 19% of the country. Here, we describe a temporal snapshot of the diet and feeding preferences of possums in a dryland habitat in New Zealand's South Island, as well as movement patterns and survival rates. We also briefly explore spatial patterns in capture rates. We trapped 279 possums at an average capture rate of 9 possums per 100 trap nights. Capture rates on individual trap lines varied from 0 to 38%, decreased with altitude, and were highest in the eastern (drier) parts of the study area. Stomach contents were dominated by forbs and sweet briar (*Rosa rubiginosa*); both items were consumed preferentially relative to availability. Possums also strongly preferred crack willow (*Salix fragilis*), which was uncommon in the study area and consumed only occasionally, but in large amounts. Estimated activity areas of 29 possums radio-tracked for up to 12 months varied from 0.2 to 19.5 ha (mean 5.1 ha). Nine possums (4 male, 5 female) undertook dispersal movements (≥1000 m), the longest of which was 4940 m. The most common dens of radio-collared possums were sweet briar shrubs, followed by rock outcrops. Estimated annual survival was 85% for adults and 54% for subadults. Differences between the diets, activity areas and den use of possums in this study and those in forest or farmland most likely reflect differences in availability and distribution of resources. Our results suggest that invasive willow and sweet briar may facilitate the existence of possums by providing abundant food and shelter. In turn, possums may facilitate the spread of weeds by acting as a seed vector. This basic ecological information will be useful in modelling and managing the impacts of possum populations in drylands.

Keywords: den use; diet; dispersal; facilitation; food preferences; home range; invasional meltdown; invasive species; survival; *Trichosurus vulpecula*

Introduction

The introduced brushtail possum (*Trichosurus vulpecula*) is a major environmental and agricultural pest in New Zealand (Cowan 2005). Browsing by possums contributes to defoliation and mortality of trees (e.g. Zotov 1949; James & Wallis 1969; Cunningham 1979; Nugent et al. 2010), and the selective nature of these impacts can alter forest composition (Fitzgerald 1976; Campbell 1990; Owen & Norton 1995; Efford & Cowan 2004). Possums also prey upon (Brown et al. 1993; James & Clout 1996; Innes et al. 1999) and compete with (Leathwick et al. 1983; Fitzgerald 1984) native fauna, and are the most important wildlife host of bovine tuberculosis (Tb) (Coleman & Caley 2000).

The demography, diet, and spatial ecology of possums have been studied extensively in forested areas and to a lesser extent in farmland in New Zealand (Green & Coleman 1986; Owen & Norton 1995; Brockie et al. 1997; Efford 1998; Efford et al. 2000; Nugent et al. 2000). That research has been important in clarifying their impacts on biodiversity (e.g. Innes et al. 1999) and their role as a reservoir of Tb (e.g. Coleman & Caley 2000; Pech et al. 2010). Such data are also needed to parameterise models to predict the impacts of possums at varying densities and under a range of management scenarios (Duncan et al. 2011), and ideally should be available for all major habitat types. However, despite the fact that around 19% of New Zealand's land mass is covered by drylands (Rogers et al. 2005), there is no published information on the diets, movements or demography of possums in these environments. Drylands are rain-shadow areas typified by admixtures of native and exotic grassland, shrubland and pasture (Rogers et al. 2005). There is widespread grazing by livestock and feral animals, although large areas of drylands have been converted to conservation estate, where livestock is no longer kept (Walker et al. 2008). Because of the biotic and abiotic features of these areas, the ecology and behaviour of dryland possums might be expected to differ substantially from those in other environments, potentially influencing the role of possums as a vector of Tb.

As part of a study designed to improve possum control, we aimed to (1) describe a snapshot of the diet and broad feeding preferences of brushtail possums in a dryland environment, (2) describe their movement patterns (activity areas and dispersal distances), and (3) estimate their annual survival rates. We also briefly explored spatial patterns in the capture rate of possums. Such information is necessary for modelling and managing the impacts of possums in dryland environments.

Materials and methods

Study area

Molesworth Station is a large (183 000 ha) grazing property in the north-east of New Zealand's South Island (42º S, 173º E). The study area encompassed most of the property, ranging from the source of the Wairau River in the west to the boundary with Muller and Muzzle stations to the east. Although it has been public conservation land since 2005, Molesworth is still managed by Landcorp Farming Limited as a working cattle station. In addition to possums, herbivores present include cattle (*Bos taurus*), goats (*Capra hircus*), red deer (*Cervus elaphus scoticus*), chamois (*Rupicapra rupicapra*), rabbits (*Oryctolagus cuniculus*), hares (*Lepus europaeus occidentalis*) and feral pigs (*Sus scrofa*).

Surrounded by mountainous terrain (altitude 549–2100 m), the western areas of Molesworth Station endure a harsh continental climate of extreme temperature fluctuations between summer, when temperatures can exceed 30ºC, and winter, when deep snow is common. A strong rainfall gradient exists on the property with average rainfall ranging from 3000 mm in western areas to 670 mm in the east. Reflecting that gradient in climate, cattle are grazed in the wetter, higher altitude western portion of the station in summer, and the eastern parts in winter.

The drier regions include vegetation such as woody shrublands dominated by either native matagouri (*Discaria toumatou*) or introduced sweet briar (*Rosa rubiginosa*) interspersed with gravel scree. Short-tussock (*Agrostis capillaris*) lands are generally restricted to valley floors or lower mountain slopes and have in places been oversown with introduced pasture grasses, while headwaters and higher altitudes support tall-tussock (*Chionochloa pallens*) lands, Spaniard grasses (*Aciphylla* spp.) and mountain flax (*Phormium cookianum*). The western (wetter) areas are largely dominated by tall tussock, patches of red tussock (*Chionochloa rubra*) and a few remnants of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest.

Possum trapping

We trapped possums in January 2005 using Victor Soft Catch No.1 leg-hold traps (Woodstream Corporation, Lititz, USA) set with a white backing board and a lure of flour and icing sugar. Trapping was conducted on 42 transects to sample a broad range of altitudes and habitat types. These were randomly located in the central and eastern portion of the station (~100 000 ha) where populations were undisturbed and so likely to be at carrying capacity, and excluded the high altitude north-western corner and also all areas where possum populations had been controlled previously. Each transect ran from a ridge line to a valley floor and comprised 2–7 lines of 10 traps spaced 20 m apart with a gap of 200 m between each trap line. Transects were located by choosing 42 points within the study area at random, then identifying the first and second highest points on the nearest ridgeline. The start of the transect was placed at a random point between these. The transect ran downhill, through the first random point, until it reached the valley floor. Transects varied in length from 1 to 3 km and comprised a total of 1570 traps. For each trap site, we recorded a GPS location, altitude and an assessment of habitat cover. Within a 10-m radius of each trap site, the percentage cover of the four most extensive habitat types was estimated visually. Cover classes were: bare ground; flat weeds / low herbs / *Hieracium*; sweet briar; matagouri; mānuka/kānuka; *Coprosma* / native scrub; willow; pine; beech; solid rock; scree; gravel; short tussock; tall tussock; improved pasture; other.

Traps were checked for two consecutive days, and all possums captured were sexed, marked with an ear-tag and released. When calculating capture rates, we deducted half a trap-night for each capture of a non-target animal and for each trap that was sprung without a capture. On the third day, the traps were replaced with cyanide paste placed at 20-m intervals along each transect (including between trap lines). Cyanide was left in place for two nights, after which the possums killed were collected and an ear-tag number was recorded (if previously marked) or assigned (if unmarked). Gender and GPS location were recorded for each poisoned animal.

Diet

We analysed the stomach contents of 100 possums selected at random from across the study area after cyanide baiting in January 2005. Stomach contents were analysed using the layer separation technique (Sweetapple & Nugent 1998). Contents of the pylorus were excluded because food items are highly mixed in this part of the stomach. With the aid of reference collections, food items were identified to species where possible. However, some items were placed into broader categories of forbs (herbaceous flowering plants, excluding grasses), fungi, invertebrates, and litter (e.g. small stones or dead plant fragments presumably consumed incidentally). Plant remains in the stomach were also grouped into seven classes describing the type of material represented. These were: grass and forbs; grass seed; native browse (woody leaves and stems); exotic browse; native woody fruit; exotic woody fruit; unidentified fruit. Diet was assessed according to (1) frequency of occurrence (the percentage of stomachs in which each food category was detected) and (2) percentage contribution of each food category to the dry weight of the stomach contents (after drying at 70°C for 24 h).

Analysis of foliar food preferences

We compared the percentage of various plants in the diet with their availability. Because our vegetation sampling only represented the availability of foliage, the percentage dry weights of stomach contents were adjusted to exclude non-foliar foods. Availability was assessed by calculating the mean percentage of each cover type on the 200-m trap line where each possum was caught. For the purposes of this analysis, *Gaultheria, Muehlenbeckia* and *Podocarpus* spp. were collectively classed as 'native scrub'. We used the cover class 'flat weeds' to assess availability of forbs. Individual species within these groups may vary in palatability. Food preferences were assessed using the Electivity Index, according to the formula $E_i = (r_i - n_i) / (r_i + n_i)$, where E is the Electivity Index, r_i is the percentage of food i in the diet, and n_i is the percentage of food i in the environment (Krebs 1999). The index ranges from −1 (indicating strong avoidance) to +1 (strong preference). We used bootstrap resampling (10 000 samples, with replacement) in R software (version 2.11.1, http://cran.r-project.org) to estimate 95% confidence intervals (CI) for the Electivity Index. An example of the R code for this procedure is provided in Appendix 1. We inferred selection for or against a particular food category if the 95% CI did not overlap zero.

Activity areas, dispersal and annual survival rates

In March 2005, possums were trapped and fitted with radio collars in both Leader Dale Valley (western Molesworth) and Yarra Valley (central Molesworth). In each valley, a trapping grid consisted of 10 parallel 2-km transects spaced 500 m apart in a mixture of scrub, pasture, and tussock habitat and covering a range of elevations from valley bottoms to ridgelines. Each 2-km transect consisted of five lines of 10 traps placed at 20-m intervals with a 200-m gap between trap lines. Additional traps (approximately 30 at Leader Dale and 45 at Yarra) were established in the valley bottoms and up adjacent valleys, extending for 1–3 km beyond each grid. Traps and lures were as described previously. We recorded a GPS location for each trap site.

We trapped for five nights. Captured possums were sedated with Ketamine, ear-tagged, weighed and sexed before being fitted with 10-g mortality-sensing radio collars (Sirtrack, Havelock North, New Zealand) and released. Only animals weighing >1.5 kg were fitted with collars. Animals were classed as either subadults or adults based on subjective assessment of pouch development and testes size.

From April to November 2005, animals were radio-tracked once per month from a helicopter equipped with an ATS 2100 receiver (Advanced Telemetry Systems, Asanti, USA) and a three-element aeronautical aluminium Yagi antenna attached to the helicopter skid. From November 2005 to March 2006, possums were tracked from the ground every 6 weeks to facilitate retrieval of collars that had switched to mortality mode. During each tracking session, GPS coordinates were recorded for each animal. Radio tracking was conducted during daylight hours, when possums are usually inactive in dens.

At the conclusion of the study (March 2006) those individual possums that still had working transmitters were radio-tracked from the ground and radio transmitters recovered by trapping, cyanide poisoning or shooting. Where possums were radio-tracked on foot to a daytime refuge or den, the type of refuge (e.g. shrub, burrow, etc.) was recorded.

Activity areas (100% minimum convex polygon (MCP); Mohr 1947) of possums were calculated using ArcGIS (Version 9.3, ESRI, Redlands, USA). Only animals that were located on at least four occasions were included in the analysis. We use the term activity area (as opposed to home range) because it is unlikely that such small numbers of location fixes were adequate to describe the entire home range of an animal. The low numbers of location fixes also preclude the use of more sophisticated home-range estimators. Dispersal was assessed in ArcGIS by calculating the straight-line distance between the initial trap location of each animal and its final known location (obtained from radio tracking or trapping). Animals for which this distance was ≥1000 m never returned to their original activity area after an initial long-range movement, and were deemed to have dispersed. To avoid artificially inflated estimates, pre-dispersal locations were excluded when calculating activity areas.

Survival of radio-collared possums was analysed using a nest survival model (Dinsmore et al. 2002) in Program MARK 6.0 (White & Burnham 1999). This model structure is similar to the known-fate model typically used in radio-tracking studies but differs in that the exact date of an animal's death is not known. Instead, time of death is inferred from the date the animal was found dead and the last date when it was recorded alive. Animals whose signals were lost (e.g. transmitter failure) were excluded from the analysis. We tested three candidate models in which survival (S): (1) varied by gender {S(gender)}, (2) varied between adults and subadults {S(age)}, or (3) was constant between both genders and age classes {S(.)}. We did not include a model in which S varied with both gender and age class because small sample sizes precluded meaningful estimates for some groups (e.g. subadult females; n = 3). We assessed model fit and parsimony using the modified Akaike Information Criterion for small sample sizes (AIC_c) (Burnham & Anderson 2002). The best performing model (with the highest Akaike weight and the lowest AIC_c) was used to estimate annual possum survival. During the 12-month period for which survival of possums was estimated, Molesworth Station experienced below-average rainfall (505 mm). However, mean daily maximum and minimum temperatures during each season at the nearby Hanmer Springs weather station were consistent with long-term averages (NIWA 2010).

Results

Capture rates

We trapped 279 possums across the 42 transects, giving an overall capture rate of 9% (n = 3106 trap-nights). On individual trap lines, capture rates ranged from 0 to 38%, with a strong east–west gradient. The lowest capture rates occurred in the west and south-west of the study area; the highest in the east and north-east. Possums were captured at altitudes ranging from 600 to >1600 m, but capture rate declined significantly with increasing altitude (Fig. 1). Non-target captures included ferrets (*Mustela furo*), stoats (*M. erminea*), hedgehogs (*Erinaceus europaeus*) and feral cats (*Felis catus*).

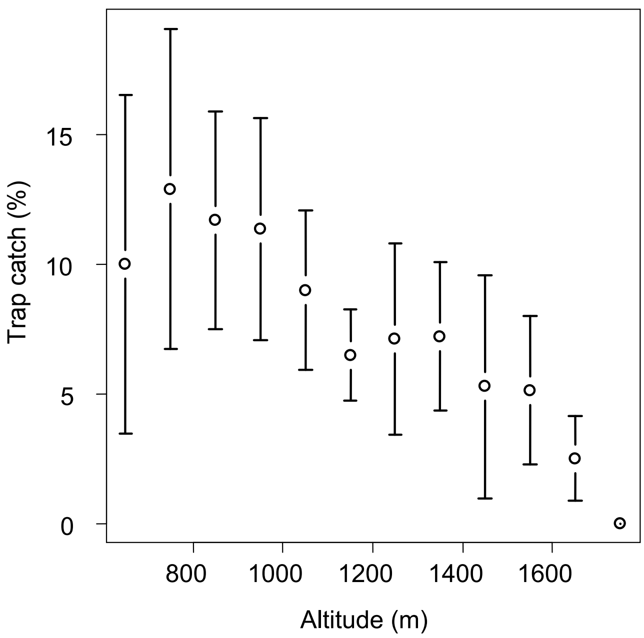

Figure 1. The capture rate of possums (*Trichosurus vulpecula*) in dryland habitats on Molesworth Station declined with increasing altitude. Error bars show 95% confidence intervals.

Diet and food preferences

The diet of possums on Molesworth Station during January 2005 was dominated by forbs and sweet briar (Table 1). Forbs aside, only eight food categories comprised more than 1% of the diet by dry weight, all of them woody species. Only a few (9–10) possums fed on tree species such as tōtara (*Podocarpus* spp.) or crack willow (*Salix fragilis*), but for those that did, these species comprised one-third to half of stomach contents on average. The mean number of food categories in each stomach was 3.6 (range 1–8).

Table 1. Food categories in the stomachs of 100 brushtail possums (*Trichosurus vulpecula*) collected in January 2005 in dryland habitats on Molesworth Station, South Island, New Zealand.

Food category	Frequency of occurrence (%)	Dry weight (%)
Plants		
Forbs	99	67.5
Sweet briar (*Rosa rubiginosa*)	64	10.9
Crack willow (*Salix fragilis*)	9	4.4
Tōtara (*Podocarpus* spp.)	10	2.7
Litter	33	2.6
Muehlenbeckia spp.	25	2.2
Gooseberry (*Ribes uva-crispa*)	10	1.9
Matagouri (*Discaria toumatou*)	14	1.7
Mountain tutu (*Coriaria plumosa*)	7	1.4
Unidentified fruits	14	<1
Cyathodes spp.	14	<1
Mountain snowberry (*Gaultheria depressa*)	8	<1
Mountain wineberry (*Aristotelia fruticosa*)	6	<1
Grass seed	2	<1
Carpet heath (*Pentachondra pumila*)	1	<1
Korokio (*Corokia cotoneaster*)	1	<1
Coprosma spp.	1	<1
Weeping māpou (*Myrsine divaricata*)	1	<1
Animals		
Invertebrates	16	<1
Eggshell	1	<1
Fungi	22	<1

Table 2. Types of plant material in the stomachs of 100 brushtail possums (*Trichosurus vulpecula*) collected in January 2005 in dryland habitats on Molesworth Station, South Island, New Zealand.

Type of plant material	Frequency of occurrence (%)	Dry weight (%)
Forbs	99	67.5
Exotic browse	71	16.9
Native browse	37	7.3
Native fruit	28	1.6
Exotic fruit	10	1.9
Unidentified fruit	10	<1
Grass seed	2	<1
Litter / non-plant material	66	4.1

Forbs were also the most common of the seven classes of plant material in the stomachs (Table 2), although native and exotic browse were important additional components of the diet. Native and exotic fruits were eaten frequently but contributed little to the dry weight of the stomach contents (Table 2).

Possums showed a preference for foliage of forbs, sweet briar and willow, which they consumed in significantly greater quantities than expected based on their availability. Possums also appeared to prefer native scrub, although this was not statistically significant. Matagouri was consumed in approximate proportion to its availability (Fig. 2).

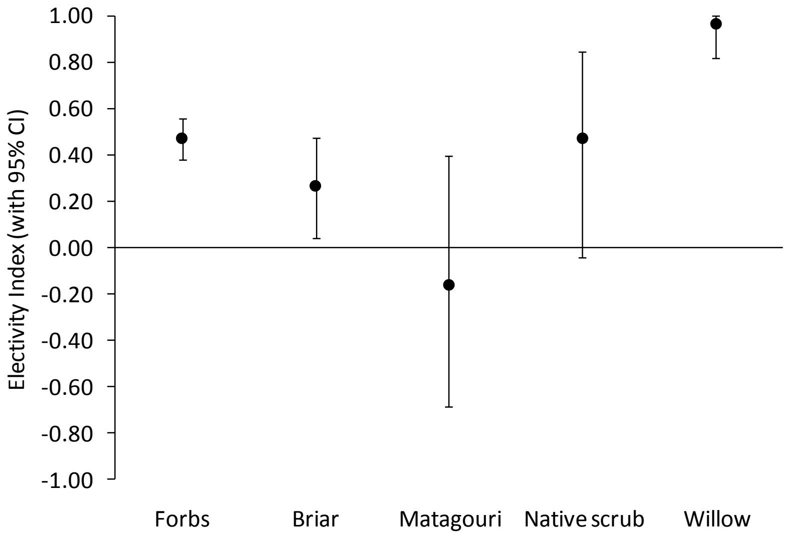

Figure 2. Positive values of the Electivity Index show that possums (*Trichosurus vulpecula*) in dryland habitats on Molesworth Station fed preferentially on forbs, sweet briar and willow. There was also an apparent preference for native scrub, although the 95% confidence interval (CI) overlapped zero, indicating some uncertainty in this result. Consumption of matagouri did not differ significantly from its availability.

Possum movements

Forty possums (21 Leader Dale, 19 Yarra) were fitted with radio collars, including 32 adults and 8 subadults. Sufficient data (4–8 points, excluding pre-dispersal locations) were obtained to estimate activity areas of 29 possums (14 male, 15 female), which varied from 0.2 to 19.5 ha, with a mean of 5.1 ha. Although the activity areas of males were larger on average than those of females (Fig. 3), a *t*-test revealed the difference was not significant ($P = 0.094$). Mean number of locations obtained (5.9 vs 6.1) and duration of radio tracking (317 vs 315 days) were similar between males and females, confirming that gender comparisons were not confounded by differences in sampling. Distance between the first and last known locations of 35 radio-collared possums ranged from 40 to 4940 m (mean 835 m) (Fig. 4). Nine possums (4 male, 5 female) undertook dispersal movements (≥1000 m). Six of these animals dispersed in March, soon after being collared. The exact times of dispersal for the remaining three animals could not be determined because we could not locate them during one or more of the monthly tracking sessions. One adult male dispersed between March and May, one subadult female between April and May, and one adult male between March and October. Dispersal distances of male (1050–4910 m; mean 2418 m) and female possums (1060–4940 m; mean 2391 m) were similar. All dispersing possums were adults at first capture except for one – a subadult female that dispersed 4940 m.

Fourteen possums were radio-tracked on foot to their dens. Five (36%) were resting in sweet briar shrubs, four (29%) in rock outcrops, two (14%) in flax bushes, two (14%) in burrows (one a rabbit burrow), and one (7%) under a large rock.

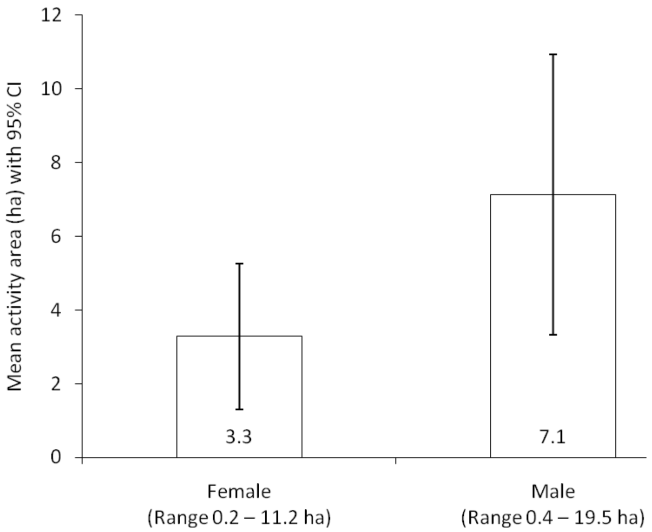

Figure 3. Activity areas of male ($n = 14$) possums (*Trichosurus vulpecula*) on Molesworth Station were more variable in size, but not significantly larger, than those of females ($n = 15$).

Annual survival rates

Of the 40 possums fitted with radio collars, 34 (18 male, 16 female) were monitored until the end of the study or until they died of natural causes. Table 3 shows the candidate models used to estimate survival. The best performing model, {S(age)}, included an effect of age on survival. This model estimated annual adult survival at 85% (CI 61–95%) while annual subadult survival was 54% (CI 20–80%). Although there was model selection uncertainty, we did not model-average because this would estimate survival separately for each gender and age class. This would result in sample sizes too small to produce meaningful estimates.

Discussion

The ecology of possums in this dryland system differed from that in other New Zealand environments in several aspects, including diet, movements and den usage. In forested areas of New Zealand, possum diet is usually dominated by canopy foliage, although other foods such as fruits may be eaten in large quantities when seasonally available (e.g. Coleman et al. 1985; Sweetapple & Nugent 1998; Nugent et al. 2000, 2001). In contrast, in the largely unforested drylands of Molesworth Station, the diet of possums during our temporal snapshot was dominated by forbs and a small number of woody shrubs, which together comprised more than 75% of the dry weight of the stomach contents. Tree species appeared to be important

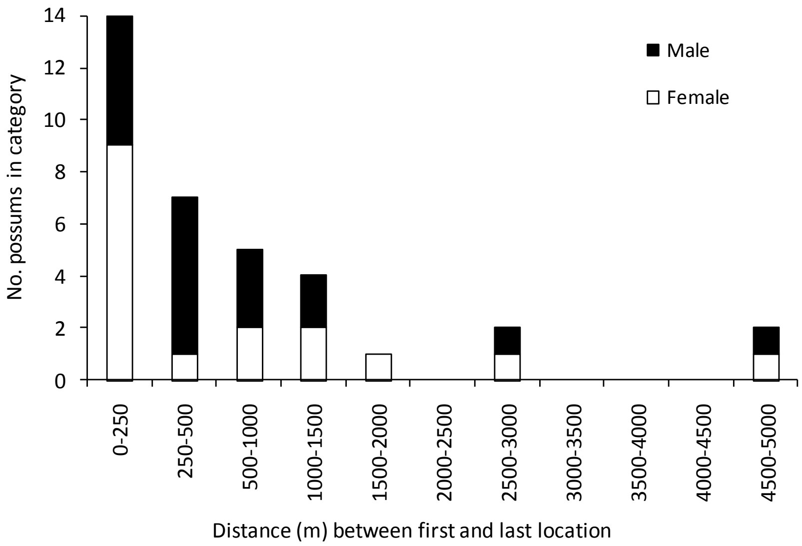

Figure 4. Distance between the first and last known locations of 35 possums (*Trichosurus vulpecula*) radio-collared on Molesworth Station from March 2005 to March 2006.

Table 3. Set of candidate models used to estimate annual survival (S) of brushtail possums (*Trichosurus vulpecula*) in dryland habitats on Molesworth Station, South Island, New Zealand. {S(age)}: survival varies between adult and subadult possums; {S(.)}: survival is constant between genders and age classes; {S(gender)}: survival varies between male and female possums. AIC_c = Akaike Information Criterion, corrected for small samples. *N* = number of parameters.

Model	AIC_c	ΔAIC_c	Akaike weight	Model likelihood	*N*	Deviance
{S(age)}	63.7958	0	0.53919	1	2	59.7945
{S(.)}	64.9014	1.1056	0.31022	0.5753	1	62.901
{S(gender)}	66.3468	2.551	0.15059	0.2793	2	62.3455

where they occurred, but were not common. Invertebrates, fruits and fungi were also frequently consumed but constituted ≤5% of the diet by dry weight. Similarly, invertebrates were frequently consumed by possums in the Orongorongo Valley near Wellington, but comprised less than 2% of the wet weight of the stomach contents (Cowan & Moeed 1987). Although eaten in small quantities, foods such as invertebrates, fungi and fruits are highly nutritious and may strongly influence the density and reproduction of possum populations (Nugent et al. 2000, 2001; Ramsey et al. 2002; Cowan 2005).

Forbs aside, introduced briar foliage was the most important dietary component during the January study period. In winter, when forbs are absent, the importance of briar (and other woody species) may increase dramatically, particularly since briar fruit ripens then. Briar seeds are commonly seen in possum scats during winter (GN & IY pers. obs.).

The frequent consumption of fruits also raises the possibility that possums are important seed dispersers in drylands. This may accelerate spread of native and exotic plants (Thorsen et al. 2009; Forsyth et al. 2010). With recent changes from livestock grazing to conservation management in many dryland areas, increased seedling survival may hasten succession from grassland to shrubland. Seed dispersal by animals such as possums may have an important influence on this succession.

Like those in other areas of New Zealand (Fitzgerald 1976, 1981), possums on Molesworth Station preferred certain food plants. Forbs, sweet briar and especially willow were consumed preferentially. Sweet briar was also frequently used for shelter. In other areas, willows also provide favoured habitat and den sites for possums (Fairweather et al. 1987; Brockie et al. 1997). The presence of willow and sweet briar may facilitate the existence of possums by providing abundant food and shelter. In turn, possums may facilitate the spread of weeds by acting as a seed vector. This would be an example of invasional meltdown, sensu Simberloff & Von Holle (1999). The possibility of such mutualisms between invasive plants and animals should be a priority for future research.

Our results suggest that possums on Molesworth Station occupy larger home ranges than those typical of forested areas in New Zealand. Whereas Cowan (2005) reported average home ranges of 1–2 ha, the mean activity area of radio-collared possums in our study was 5.1 ha. This estimate is based on small numbers of locations, and almost certainly underestimates the true size of possum home ranges on Molesworth Station. In addition, our estimates are based primarily on daytime den locations. If possums range more widely during their nocturnal activity than the area in which they den (e.g. Paterson et al. 1995), true home ranges could be much larger than our estimated activity areas. We speculate that possums in drylands may have large home ranges because resources such as food and den sites are probably much more sparsely distributed in this harsh environment compared with most forest environments. Similarly, possums in farmland can have much larger home ranges than those typical of forests (Cowan & Clout 2000).

Dispersal distances of possums on Molesworth Station were relatively small compared with other studies in New Zealand. For example, Cowan and Clout (2000) reported that dispersal movements average around 5 km, a little more than the maximum dispersal distance in our study. This result is surprising, especially as our estimated activity areas indicate that possums on Molesworth Station were highly mobile. It is possible that some dispersal movements were missed if animals had already dispersed before they were collared in March, or if collared animals moved beyond the range at which we could detect their radio collars. However, there were only six possums (15%) whose fates were unknown because of the loss of radio signal, including three adults and three subadults. It is also possible that our sampling did not detect long-range dispersal of juveniles because we collared only animals >1.5 kg.

In general, male brushtail possums disperse more frequently, but females disperse over greater distances (Cowan & Clout 2000). However, we found no difference between genders in the frequency or extent of dispersal movements (but the small number of dispersal movements recorded means that this result must be interpreted cautiously). Although most dispersers have been reported to be juveniles or subadults (Cowan & Clout 2000), all but one of the dispersing possums in our study were adults at the time of capture. However, dispersal by adult possums has occasionally been recorded in New Zealand (Efford 1991), and Winter (1976) found that shifts in home range were common among male brushtail possums in Australia until they reached 4 years of age. Although sexually mature, the dispersing animals in our study may have been young adults.

Den use by possums on Molesworth Station also differed from that in forested environments, where possums often den in trees or remnants of trees such as logs or stumps (e.g. Green & Coleman 1987; Cowan 1989). Trees are absent from most of Molesworth Station, where 50% of dens were in shrubs (sweet briar or flax), the remainder being in rock outcrops, burrows or under a rock. Similarly, in an area of mixed pasture, open savannah woodland and forest scrub on the North Island, possums frequently sheltered in flax shrubs, as well as in piles of fallen timber. They also occasionally used burrows (Paterson et al. 1995).

Similarities also existed between the ecology of possums in this dryland environment and that of other areas of New Zealand. Survival rates of adult possums on Molesworth Station were similar to estimates from other New Zealand environments (Brockie et al. 1981; Spurr 1981; Efford 1998), and the lower survival rate of subadult possums compared with adults is consistent with estimates from the Orongorongo Valley (Efford 1998, 2000). The negative association between capture rate of possums and altitude has also been noted in New Zealand forests (Coleman et al. 1980; Clout & Gaze 1984). Although our results show that capture rates of possums varied along altitudinal and longitudinal gradients, other factors such as habitat type are also likely to have influenced abundance. A more sophisticated spatial model of capture rates is the subject of a forthcoming paper.

In summary, brushtail possums on Molesworth Station differed from those in other New Zealand environments in terms of their diets, activity areas and den use. These differences most likely reflect differences in the availability and distribution of resources between drylands and forest or farmland. Despite these differences, survival rates were similar to those elsewhere in New Zealand. This basic ecological information is useful in modelling and managing the impacts of possum populations in drylands.

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Appendix 1. Example of the R code used to estimate the Electivity Index and associated 95% confidence intervals

```
#Input data:
rm(list=ls())
data <- read.table("forbs.txt",header=TRUE)
attach(data)
consumed<- na.omit(data$X.Vol)
available<-na.omit(data$X.Cover)

#Parametric bootstrap and calculation of Electivity Index:
EI<-numeric(10000)
for (i in 1:10000)
{
vol <- mean(sample(consumed,replace=T))
cover <- mean(sample(available,replace=T))
EI[i]<- (vol-cover)/(vol+cover)
}
EI<-na.omit(EI) # Electivity Index
CI <-quantile(EI,c(0.025,0.5,0.975)) #Median and 95% confidence interval
```