NEW ZEALAND JOURNAL OF ECOLOGY

RESEARCH

Habitat-specific densities of urban brushtail possums

Charlotte R. Patterson[1]*, Philip J. Seddon[1], Deborah J. Wilson[2] and Yolanda van Heezik[1]

[1]Department of Zoology, University of Otago, PO Box 56, Dunedin 9016, New Zealand
[2]Manaaki Whenua – Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand
*Author for correspondence (Email: crpattrsn@gmail.com)

Published online: 24 July 2021

Abstract: Invasive mammalian pests threaten biodiversity globally across a diverse range of habitats. The unique combination of resource subsidies and disturbance in cities can provide favourable conditions for invasion. Recent interest in urban biodiversity enhancement has increased the demand for effective urban pest control, but efforts are often hampered by a lack of understanding of the ecology of urban invasive mammals. The Australian common brushtail possum (*Trichosurus vulpecula*) has invaded most New Zealand landscapes, including urban areas, and is a nationally significant pest species. Recent shifts in national pest control and conservation priorities demand an assessment of the capacity for urban areas to harbour possum populations. We estimated the density of possums across three representative habitat types within the city of Dunedin, New Zealand: an urban forest fragment and two residential areas of varying vegetation quality. Possums were live-trapped and camera-trapped over eight days at each site in late summer to early autumn. Spatially explicit capture-recapture methods were used to estimate density at each site, and "minimum number alive" estimates were also calculated. Our estimate suggests that the forest fragment supported possums at a density (3.1 ha^{-1}) capable of inflicting harm on resident native wildlife, but this density was low compared with non-urban estimates in the same forest type, suggesting a possible influence of disturbance from human activity in and around the fragment. Few possums were caught at the two residential sites (0.1 ha^{-1} at each), and behavioural avoidance may have reduced capture success there. Our estimates confirm that urban areas are an important habitat for possums, and our study provides the first rigorous estimates of urban possum density, which can be incorporated into predictive modelling and other methods of control planning.

Keywords: capture-recapture, density, invasive species, possum, *Trichosurus vulpecula*, urban ecology

Introduction

Urban areas are unique and challenging environments for wildlife, characterised by high levels of disturbance, habitat fragmentation and patchy resource distribution (Harper 2005; Lowry et al. 2013). As a consequence, cities tend to support wildlife communities that are less biodiverse and abundant than other habitats (Chace & Walsh 2006; Aronson et al. 2014). Nevertheless, urban areas can sustain native biodiversity, including threatened species (Angold et al. 2006; Aronson et al. 2014; Gallo et al. 2017; Woolley et al. 2019), and urban biodiversity provides opportunities for people to experience and connect with nature at a time when human-nature interactions are declining (Dearborn & Kark 2010; Soga & Gaston 2016). The unique conditions of cities also favour traits common to invasive species – namely, behavioural flexibility and a tolerance of disturbance (Lowry et al. 2013). As such, species that thrive in cities are frequently invasive (McKinney 2006). Artificial food sources and shelter enable some invasive species to exist at high densities in cities (McKinney 2006) where they impact native wildlife through predation and competition (Chace & Walsh 2006; Shochat et al. 2010). Efforts to control invasive species in urban areas are therefore crucial for protecting and restoring important urban wildlife. However, research is needed to understand the behaviour and population processes of invasive species in cities (Gallo et al. 2017; Russell & Stanley 2018), as it cannot be assumed that these processes will be consistent with those in other habitats.

The common brushtail possum (*Trichosurus vulpecula*; 'possum' herein), an arboreal marsupial of the family Phalangeridae, is a significant pest species in New Zealand (Clout 2006). Introduced from Australia in the 1800s, possums are now present across most of the country (Cowan 2005). Possums are highly destructive folivores that have complex impacts on trees in all New Zealand forest types (Payton 2000). They also prey on and compete with native birds and invertebrates (Sadlier 2000; Clout 2006). Possums occupy urban areas in Australia and New Zealand (Matthews et al. 2004; Adams et al. 2013; Eymann et al. 2013), and although possum densities have generally declined across their native range, possums can be abundant in Australian cities (Matthews et al. 2004; Eymann et al. 2013; Carthew et al. 2015). Characteristics enabling this success include behavioural flexibility, which allows possums to exploit novel resources, and a high tolerance

DOI: https://dx.doi.org/10.20418/nzjecol.45.27

of disturbance (Adams et al. 2014; Carthew et al. 2015). The use of novel den sites (buildings), and human-provided supplementary food resources (compost heaps, fruit trees), are examples of this adaptive behaviour (Statham & Statham 1997; Harper 2005; Carthew et al. 2015).

Population density is an important metric of possum impact, as their interactions with, and impacts on native and non-native fauna tend to increase with density (Efford 2000; Duncan et al. 2011; Holland et al. 2013). Possum home range size, productivity, dispersal distance, and other population characteristics also change with density (Isaac & Johnson 2003; Whyte et al. 2013; Richardson et al. 2017). Possum density in New Zealand tends to be habitat-specific, reflecting the availability of key resources, including food, den sites, and tree cover (Efford 2000). Habitat-specific possum densities across New Zealand have been estimated to range from < 1 ha^{-1} to > 20 ha^{-1} (Efford 2000; Rouco et al. 2013). However, there are no urban possum density estimates for New Zealand, despite the potential for possums to impact urban-based native biodiversity and increasing interest in urban mammalian pest control (Russell et al. 2015). Urban possums appear to distribute themselves according to food and den site availability, leading most to occupy home ranges that intersect forest fragments (Statham & Statham 1997; Harper 2005; Harper et al. 2008; Adams et al. 2014). However, possums are also capable of living within vegetated urban residential areas, entirely independent of urban forest fragments (Adams et al. 2014). Residential areas and urban forest fragments therefore both represent habitat for possums.

Here, we estimate the density of possums across three urban habitat types in the city of Dunedin, New Zealand, using spatially explicit capture-recapture methods. We aimed to explore distinct habitat types that represent the heterogeneity of conditions and resources in cities. These habitat types were an urban forest fragment and two residential areas, one with high and one with moderate vegetation cover and structural complexity. We expected that possums would be present in each habitat at low to moderate densities that reflected the availability of foliage, their primary food item, although it was also hypothesised that human disturbance such as pedestrians and vehicles might play a role in limiting densities at each site. This research was conducted with the aim of gathering baseline data of urban possums in New Zealand in order to effectively plan and achieve future possum control and biodiversity outcomes. These data would also improve predictive possum models, which to date have made the unsupported assumption that possum density in urban areas is zero (Warburton et al. 2009; Shepherd et al. 2018; Lustig et al. 2019).

Methods

Study sites

Capture-recapture trapping took place between 1 February and 15 April 2019 across three sites within the city of Dunedin, New Zealand (45°52′S, 170°30′E) (Fig. 1). The three sites represented three urban habitat types, as defined by a Dunedin habitat map shapefile (Freeman & Buck 2003; Mathieu et al. 2007): (1) "Forest fragment", a closed-canopy native and exotic tree stand surrounded by an urban landscape, (2) "Residential I", residential areas with greater than one third of the property comprised of mature, structurally complex gardens containing an assortment of lawns, hedges, shrubs, and large established trees, and (3) "Residential II", residential areas with greater than one third of the property comprised of less structurally complex gardens dominated by lawns. Green cover in Residential I totals about 70%, and in Residential II it ranges between 42% and 50% (Freeman & Buck 2003).

The forest fragment site Jubilee Park (9 ha) is an amenity area managed by the Dunedin City Council, situated close to the centre of the city (Fig. 1). The park is bordered by roads and residential housing, and is part of the Dunedin Town Belt, a 200 ha green belt spanning the central suburbs. The vegetation of Jubilee Park is a mix of regenerating native broadleaved and fern species, particularly *Pittosporum* spp., *Griselinia littoralis* and *Fuchsia excorticata*, which comprise the mid and lower layers of undergrowth, along with an emergent canopy of exotic tree species (*Pinus* spp. and *Salix* spp.). The last possum control implemented at Jubilee Park by the Dunedin City Council was eight months prior to this study; the park was subject to periodic control before then. Jubilee Park was deemed representative of a typical New Zealand urban forest fragment, as these often have a history of intermittent possum control.

At Maori Hill, the Residential I site (7 ha), and Wakari, the Residential II site (7 ha), traps were placed in private backyards (Fig. 1). The suburb of Maori Hill has a low housing density and the typical section size is moderate to large (700–1000 m^2). Many houses have fruiting trees and open or closed compost heaps. The average distance from traps to the nearest point of the Dunedin Town Belt, calculated in QGIS v 3.6.2 (QGIS Development Team 2019), was 231 m (SD 75 m). Close proximity to a forested area is positively associated with possum occupancy, and most likely to be a feature of Residential I habitat (Adams et al. 2013). At the Wakari site, gardens were of a moderate size (500–800 m^2). Some backyards at both residential sites had compost heaps, vegetable gardens and fruit trees.

Trapping protocol

Trapping was conducted under University of Otago Animal Ethics Committee approval AUP-18-201, and with permission from the Dunedin City Council and affected property owners. The trapping grid at each site comprised Grieve Wrought Iron wire live-capture cage traps, each with a folding door triggered by a pendulum hook, placed at roughly 30 m spacing (Efford 2004; Efford & Cowan 2004; Nugent et al. 2011). At Jubilee Park traps ($n = 70$) were placed according to locations determined using a Garmin GPS unit (Fig. 1). At Maori Hill ($n = 64$) and Wakari ($n = 65$) a trapping grid was constructed based on property locations aligning with a grid created in Google Earth Pro (https://www.google.com/earth/). The final grid at these residential sites avoided roads and other obstacles and was in part determined by access permission from property owners (Fig. 1).

Each site was trapped for eight consecutive nights. Possums are likely to visit all parts of their home range over such a period, increasing the likelihood of detection (Adams et al. 2013). Traps were baited with cinnamon-coated apple and lured with a 50:50 flour and icing sugar blaze extending 30 cm from the mouth of the trap. Traps were checked each morning and re-baited when the bait had been removed by possums or other animals, or every three days. Captured possums were photographed and then anaesthetised with 5% isoflurane gas and 1.5% oxygen using a SHOOF Portable Anaesthetic Machine (SHOOF International). Individuals were given two ear tags with unique identifier codes (National Band and Tag Co., Kentucky, USA, size 1005-3, style 893) before

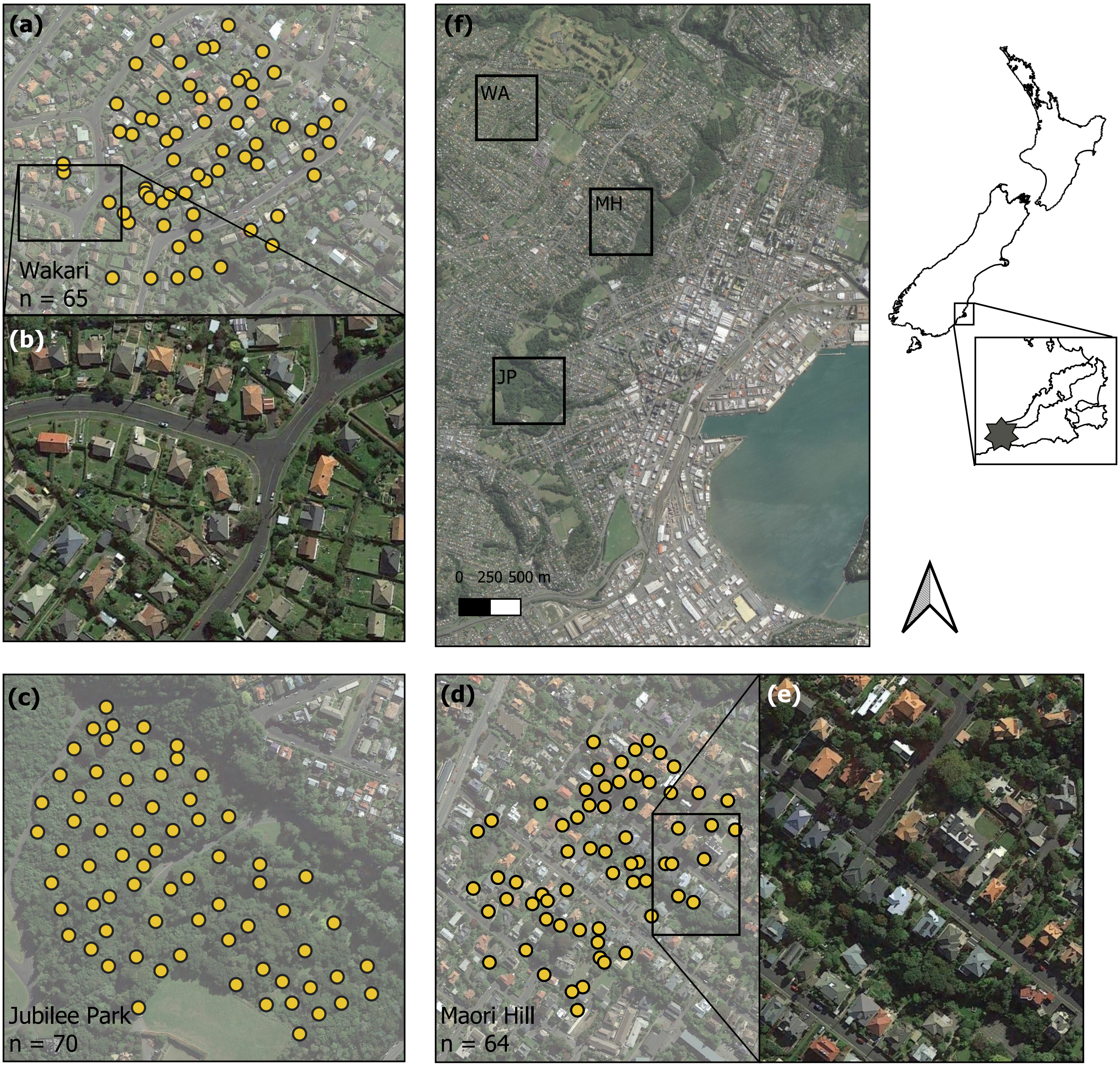

Figure 1. The location of three trapping grids in the city of Dunedin, representing three urban habitat types, where capture-recapture of possums took place. Traps were spaced c. 30 m apart, with locations determined by study area and access constraints. The three sites were: (1) Wakari (WA), a residential area with properties dominated by lawns and small shrubs (a) (b); (2) Jubilee Park (JP), an urban forest fragment (c); and (3) Maori Hill (MH), a residential area with well-vegetated properties dominated by trees and shrubs (d) (e). The location of the grids in Dunedin is shown in (f).

being released near their capture location. On two occasions at Jubilee Park possums escaped untagged, but re-sight by photo identification was deemed sufficient as a recapture method for these individuals as both had unique scarring on their face and ears that was visible on images. Recaptured animals were recorded and released; twice an individual had lost both ear tags, but could be identified by unique physical traits such as ear shape, colouration pattern and visible scarring.

Due to low capture rates at Maori Hill and Wakari, camera traps were added for the last four and three nights at these sites respectively. Cameras (Bushnell Trophy Camera model 119836, brown; n = 12 at each site) were placed at every fifth trap location, except where there were no appropriate attachment surfaces. Cameras were placed 30–60 cm above the ground, 2–7 m from the trap, and were set to video 30 s of footage when motion sensors were activated, with 10 s intervals between videos. Cameras were activated at 18:00 each day and checked the following morning.

SECR analysis

The density of possums at the three sites was estimated via likelihood-based spatially explicit capture-recapture (SECR; Borchers & Efford 2008) with the secr package v. 4.3.0 (Efford 2019) for R v. 3.5.2 (R Core Team 2018). Because there were no recaptures in the cage traps at Maori Hill and Wakari, the SECR model parameters were not identifiable when these data were analysed independently. Instead, the Maori Hill and Wakari data were fitted to a multi-session model with the Jubilee Park data. Each site's population was assumed to be closed (no births, deaths, immigration or emigration) during the short trapping periods (Otis et al. 1978). SECR models require a definition of the "area of integration": the region across which the activity of target animals can be centred, and across which integrals in the likelihood function are approximated by summations. This means non-habitat can be excluded in fragmented landscapes, minimising the potential for underestimation of habitat-specific densities (Borchers & Efford 2008). The area of integration must be large enough to encompass all individuals with non-negligible detection probabilities (Efford 2004; Royle & Young 2008). Because Jubilee Park was located within a heterogeneous urban landscape, it was necessary to specify areas of forest fragment habitat and non-habitat by creating a "habitat mask" object in QGIS using the National Landcover Database v. 4.1 shapefile (https://lris.scinfo.org.nz/layer/48423-lcdb-v41-land-cover-database-version41-mainland-new-zealand/) (Hooker et al. 2015; Braczkowski et al. 2016). A buffer width of 300 m was chosen based on pre and post model-fitting assessment (secr functions "suggest.buffer" and "mask.check"), and resulted in a total mask area of 29 ha (Fig. 2). A 300 m buffer was also used for the trap locations at Maori Hill (mask area = 64 ha) and Wakari (mask area = 64 ha).

Model selection

We used the half-normal detection function to depict the probability of capture of an individual possum, following precedent from prior possum SECR analyses (Efford 2004; Rouco et al. 2013; Richardson et al. 2017). Several models with varying spatial detection parameter values were compared, to represent possible alternative behaviours affecting the trapping process, including "trap-shy" or "trap-happy" behaviour (Borchers & Efford 2008; Rouco et al. 2013). Variation was applied only to the parameter g_0 – the one-night probability of capture of an individual in a trap at the centre of its home range. The parameter σ, which determines the spatial decay of the half-normal home range kernel, was kept constant. The multi-session model assumed that these detection parameters were the same for all sites, whereas density was allowed to vary. The models considered were:

(1) a null model, where g_0 was constant;
(2) model b which simulated a permanent step-change behavioural response to capture, where animals that had been captured had an altered detection probability for the remainder of the trapping period (Otis et al. 1978; Borchers & Efford 2008);
(3) model bk, a permanent behavioural response to capture that was specific to trap location;
(4) model B, a transient behavioural response to capture that affected only the next trapping occasion;
(5) model Bk, a location-specific transient behavioural response to capture.

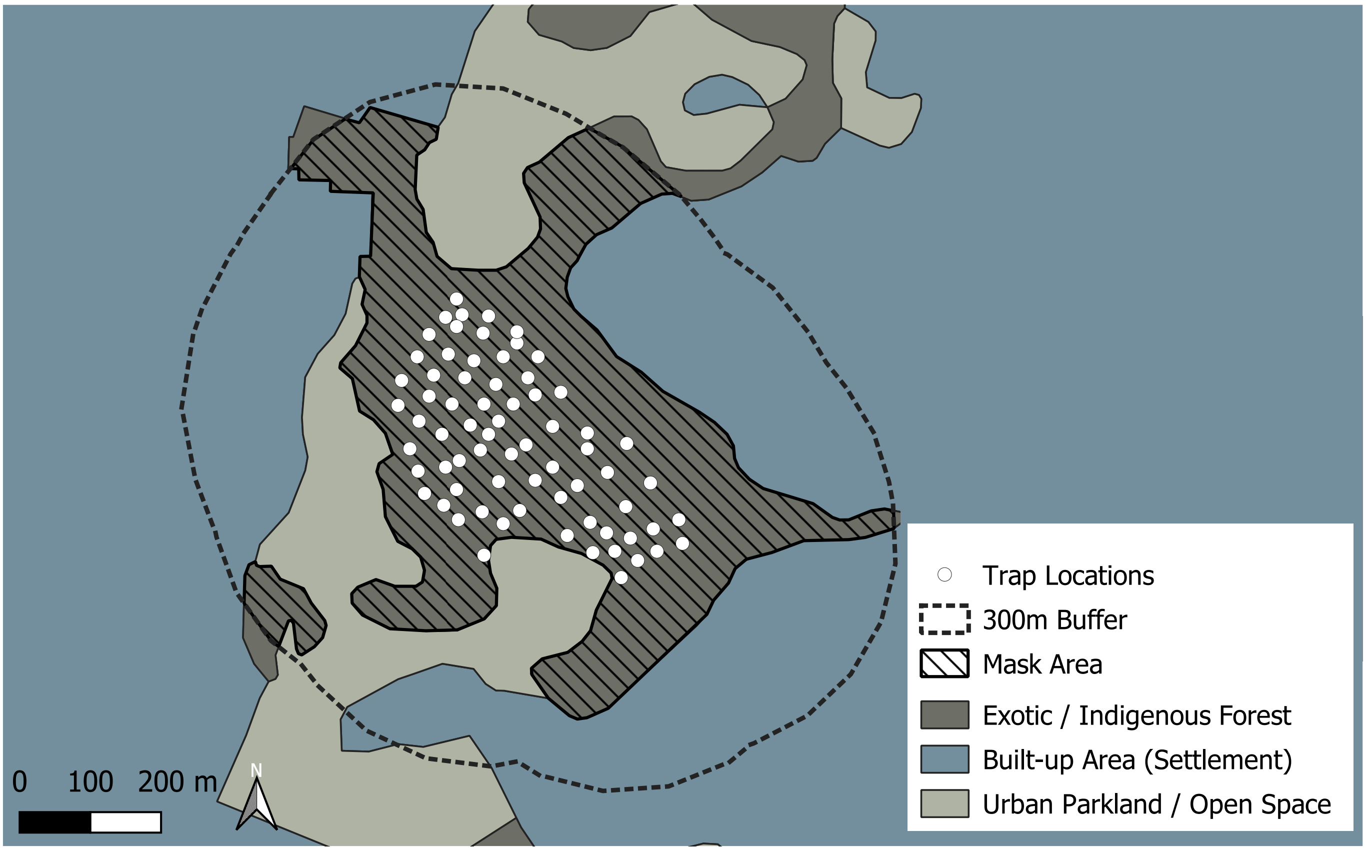

Figure 2. The polygon shapefile created in QGIS describing the habitat types of Jubilee Park, an urban forest fragment in the centre of Dunedin, and the surrounding area. A 300 m buffer around the trap locations was used to delineate a habitat mask, within which computation of density was undertaken via Spatially Explicit Capture-Recapture (SECR). This habitat mask excluded non-forest-fragment habitat to reduce the risk of underestimating habitat-specific density at this site.

Model fitting was carried out by maximising the likelihood, assuming a multi-catch estimator which has been shown to be appropriate for single-catch traps when trap saturation is low (< 60% each night) (Distiller & Borchers 2015). Models were compared via Akaike's Corrected Information Criterion (AICc) (Hurvich & Tsai 1989). However, if a model included an additional parameter, and increased AICc by about 2, the model was classified as having an "uninformative parameter" (Burnham & Anderson 2002; Arnold 2010) and was not considered further. Possum density was calculated by model-averaging (Burnham & Anderson 2002) the estimated densities from the remaining models.

Minimum density based on minimum number alive

To provide another type of estimate for comparison that incorporated data from the camera traps at Maori Hill and Wakari, live-capture and camera trap information were combined to calculate a "minimum number alive" (MNA) estimate for possums at each site (Pickett et al. 2005). At Jubilee Park only live-capture data were used. We considered effective trapping areas (ETA) for each site to include the trapped area plus a boundary strip equivalent to home range radius (Dice 1938; Wilson et al. 2007). Minimum convex polygons were calculated around the trap locations in QGIS. Because accurate movement patterns were unlikely to be revealed by the few captured individuals at the Maori Hill and Wakari sites (Parmenter et al. 2003; Foster & Harmsen 2012), we based the boundary strip width on mean (± SE) home range of possums (3.54 ± 0.45 ha) estimated from GPS tracking in residential Dunedin gardens in 2010–2011 (Adams et al. 2014). Assuming a circular home range area, the buffer width of the average home range radius was added to the trapping area to create the final ETA for each site (Foster & Harmsen 2012). Minimum density was then calculated as the MNA divided by the ETA.

Results

In total 52 individual possums were captured at the Jubilee Park site (Table 1). We recorded 42 recaptures, with most individuals being re-captured once or twice. The b model was the top-ranking model based on AICc scores; all other models were within 2–3 AICc units of the b model and had moderate AICc weights (Table 2), but all except the null and b models were classified as having an uninformative parameter (Burnham & Anderson 2002; Arnold 2010). Models with uninformative parameters were not considered further, and the possum density (± SE) at Jubilee Park derived by model-averaging the null and b models was 3.1 ha^{-1} (± 0.6).

Only two individual possums were identified at Maori Hill, and five at Wakari. One individual at Maori Hill was re-sighted by camera trap on two separate nights. At Wakari, one individual was re-sighted by camera trap on two consecutive nights, while another was seen by camera trap at two different traps on the same night. Model-averaged possum densities (± SE) were 0.1 ha^{-1} (± 0.1) at Maori Hill and 0.1 ha^{-1} (± 0.1) at Wakari.

Due to the final trap spacing, the ETA was smaller at Maori Hill (19.4 ha) than at Wakari (23.4 ha) and Jubilee Park (24.4 ha). Estimated minimum possum density was 2.1 ha^{-1} at Jubilee Park, 0.1 ha^{-1} at Maori Hill and 0.2 ha^{-1} at Wakari (Table 1).

Discussion

The estimated density of possums varied across three urban sites, highlighting the importance of fine-scale habitat differentiation in determining the relative densities of geographically-close urban possum populations. The value we obtained at Jubilee Park using MNA as opposed to SECR was lower, as expected, since undetected individuals are not accounted for in MNA. The SECR and MNA values were similar at the residential sites, due to the very low number of captures and recaptures there. As predicted, the forest fragment supported possums at a moderate density, although the density was lower than expected for a mix of native broadleaved and exotic species. Previous studies in exotic (oak *Quercus robur* and sycamore *Acer pseudoplatanus*) and mixed broadleaved forests estimated densities of 7 and 10 individuals ha^{-1}, respectively (Nugent et al. 2010; Whyte et al. 2013). Our SECR estimate of 3.1 ha^{-1} is more similar to estimates for radiata pine (*Pinus radiata*) forest (1–2.5 ha^{-1}) (Efford et al. 2005; Whyte et al. 2013) and native southern beech (*Nothofagus* spp.) forest (2–5.6 ha^{-1}) (Sweetapple 2008; Pech et al. 2010). Urban forest fragments are subject to conditions that are likely to reduce their habitability, including disturbance from humans and domesticated animals, noise and light pollution, and edge effects extending from the

Table 1. The summarised results of density estimates of possums at three sites of varying vegetation quality and residential influence within the city of Dunedin, including the total number of individual possums caught and recaptured (in traps, and also considering re-sightings via camera trap as recaptures), and estimates of the spatial parameters g_0,the one-night probability of an individual being caught in a trap at the centre of its home range, and σ, a measure of home range size. Methods used were spatially explicit capture-recapture (SECR) or minimum number alive (MNA) within an effective trapping area (ETA). In the MNA method, minimum density was calculated as MNA divided by ETA.

Site	Total indiv.	Total recap.	Method	Density (ha^{-1}) (± *SE*)	$\hat{g}_0$ (± *SE*)	$\hat{\sigma}$ (± *SE*)
Jubilee Park	52	42	SECR	3.1 (*0.56*)	0.02 (*0.008*)	80.35 (*8.188*)
			MNA	2.1		
Maori Hill	2	3	SECR	0.1 (*0.09*)	0.02 (*0.008*)	80.35 (*8.188*)
			MNA	0.2		
Wakari	5	2	SECR	0.1 (*0.05*)	0.02 (*0.008*)	80.35 (*8.188*)
			MNA	0.1		

Table 2. AICc comparison of secr models of possum density at three sites (JP = Jubilee Park, MH = Maori Hill, WA = Wakari) in Dunedin. Models b, bk, Bk and B represent alternative behavioural responses to capture (see Methods for descriptions). ~1 indicates a parameter was kept constant. $\hat{D}$ is a density estimate, $\hat{g}_0$ is the one-night probability of an individual being caught in a trap at the centre of its home range, $\hat{\sigma}$ is a measure of home range size, and ΔAICc is the change in AICc score relative to the best-performing model. The models with the lowest AICc and no uninformative parameters were chosen as the top-performing models, and possum density was estimated by model averaging.

Model	Parameters	Site	$\hat{D}$	$\hat{g}_0$	$\hat{\sigma}$	Log likelihood	AICc	ΔAICc	Model weight
b	$g0{\sim}1\ \sigma{\sim}1$	JP MH WA	2.91 0.10 0.10	0.03	80.04	−461.86	935.72	0.00	0.38
null	$g0{\sim}b\ \sigma{\sim}1$	JP MH WA	3.40 0.12 0.12	0.02	80.72	−463.26	936.52	0.29	0.33
bk	$g0{\sim}bk\ \sigma{\sim}1$	JP MH WA	3.43 0.12 0.12	0.02	81.83	−463.09	938.19	2.46	0.11
Bk	$g0{\sim}Bk\ \sigma{\sim}1$	JP MH WA	3.41 0.12 0.12	0.02	80.99	−463.21	938.43	2.71	0.10
B	$g0{\sim}B\ \sigma{\sim}1$	JP MH WA	3.38 0.12 0.12	0.02	80.70	−463.25	938.50	2.78	0.09

corresponding urban matrix (Mörtberg 2001; McDonnell et al. 2008; Caryl et al. 2013). These conditions may limit the density of possums in Jubilee Park. Nevertheless, our estimate of possum density there reinforces the importance of urban forest fragments as habitat for possums.

Our findings support the conclusion of Adams et al. (2013), that possums in Dunedin frequent urban habitats that also act as refugia for taxa such as native birds (van Heezik et al. 2008). As well as the risk of predation of native birds' eggs and chicks, possums at Jubilee Park may be sufficiently abundant to trigger die-back of native vegetation. Holland et al. (2013) demonstrated that possums can cause browsing damage that exceeds a tree's "damage threshold", at which point irreversible damage has occurred, generally resulting in the death of the tree. At some sites this threshold was reached at densities of 3–4 individuals ha^{-1} (Holland et al. 2013). At their observed density in Jubilee Park, possums might cause this damage threshold to be crossed for plant species in Dunedin forest fragments, leading to die-back (Rose et al. 1992; Holland et al. 2013), despite semi-regular possum control operations by the Dunedin City Council.

We expected that possums would be more abundant in Residential I habitat than in Residential II. Residential I habitat tends to include gardens with vegetation that is structurally more complex than Residential II habitat, and is more likely to include mature trees, hedges, and shrubs (Freeman & Buck 2003). These features potentially provide more browse for possums, as well as refuges from predators such as dogs, and den sites. Being closer to nearby forest fragments, which are frequently occupied by possums in Dunedin (Adams et al. 2014), also led us to expect higher possum densities in Residential I habitat. However, contrary to our predictions, the two residential sites had similarly low capture rates. The SECR-derived possum densities at the two residential sites were lower than any recorded densities in New Zealand, but were most similar to the grassland/shrubland estimates of Rouco et al. (2013) and Glen et al. (2012) (0.4–0.7 ha^{-1} and 1.7 ha^{-1} respectively), as well as some of the lower density estimates in *Nothofagus* spp. southern beech forest (0.5 ha^{-1}) (Clout 1977; Clout & Gaze 1984). In Australia, comparably low densities have been recorded at locations primarily comprised of *Eucalyptus* spp., including sites around Canberra (0.49 ha^{-1}) (Dunnet 1964), Tasmania (0.31 ha^{-1} and 0.04 ha^{-1}) (Hocking 1981; le Mar & McArthur 2005), New South Wales (0.44 ha^{-1}) (How 1972), and South-Western Australia (0.28–2.84 ha^{-1}) (How and Hillcox 2000). Some of these low densities can be attributed to anthropogenic habitat degradation, disturbance, or predation, while others simply indicate poor natural habitat quality for possums (le Mar and McArthur 2005).

The low capture rates at the residential sites suggest that relatively few possums live in these habitats. Challenges associated with residential areas such as disturbance from human activity might limit possum occupation to individuals that are particularly tolerant or behaviourally flexible. Individuals of a range of species living in urban areas often display distinct behavioural differences to their counterparts in other habitats, with more bold or explorative individuals representing the majority of individuals in urban populations (Lowry et al. 2011; Lowry et al. 2013). Conversely, there could be more possums at these sites than trapping suggests, due to individual avoidance of trapping devices. Some evidence supports this. Some prior observations indicate that urban possums were difficult to recapture (< 5% success rate) and were trap-shy (Statham & Statham 1997; Adams et al. 2014). Householders in this study claimed that evidence of possums was routinely seen in their backyard, or that possums denned in their house roof, and we saw physical evidence (scat, browsing damage) and film footage of recent possum presence at sites where we captured none. Nevertheless, while possum densities appeared to be lower in the residential areas than in the forest fragment, these areas represent important habitat within the home range of at least some individuals. Although we were unable to estimate separate detection functions for our three study sites due to low trapping rates in residential areas, future studies may be able to distinguish differences in detection between residential environments and urban forest fragments.

The data we present here confirm the capacity for parts of urban habitats to harbour significant possum populations, but this study is only a snapshot density estimate of single populations at three sites in one season (late summer–early autumn). Possum density fluctuates seasonally with the availability of food resources and timing of breeding periods (Efford 2000; Efford & Cowan 2004). Extrapolation of our results to other similar habitat types should be done with caution. Ideally, long-term density estimates should be made for urban habitats across a range of sites, as our findings suggest the potential for important differences among urban habitats and between urban habitats and other ecosystems.

We have shown that urban habitats of differing vegetation cover and residential character harbour possums at varying densities. As in other habitats, vegetation cover may be the most important factor determining possum occupation, with moderately high possum density in a forest fragment and low densities at residential sites. The forest fragment supported possums at a density capable of harming vegetation and resident native wildlife, but in the lower range of expected density for the habitat type, suggesting a possible influence of anthropogenic disturbance. Possums were at low numbers in two residential sites, but trap avoidance could have resulted in under-estimates of density in these highly modified and disturbed areas. The density estimates we have derived here can be used to inform predictive possum models, so as to better represent urban areas as habitat for possums and plan control accordingly.

Acknowledgements

We thank Aalbert Rebergen from DCC for providing contracting help, and Dave McPhee for advice in the field on the first day of trap set-up. Thanks to Murray Efford and others in the SECR community for helpful comments during the analysis stage, and Stephanie Godfrey who provided us with anaesthesia equipment. Thanks to all who assisted with fieldwork, particularly Scott Forrest, Tim Plaisted, Taylor Hamlin and John Ward, and those Dunedin residents who allowed access to their properties. CRP was supported in this work by a University of Otago Master's Research Scholarship and an Otago Council Inc Scholarship in Science. DJW received funding from the Ministry of Business, Innovation and Employment's Strategic Science Investment Fund for Crown Research Institutes.

Author contributions

CP, YvH, PS & DW conceptualised the research. CP collected the data, carried out the analyses and produced a first draft. All authors contributed to editing and revisions.

References

Adams AL, Dickinson KJM, Robertson BC, van Heezik Y 2013. Predicting summer site occupancy for an invasive species, the common brushtail possum (*Trichosurus vulpecula*), in an urban environment. PLOS ONE 8: e58422.

Adams AL, Recio MR, Robertson BC, Dickinson KJM, van Heezik Y 2014. Understanding home range behaviour and resource selection of invasive common brushtail possums (*Trichosurus vulpecula*) in urban environments. Biological Invasions 16: 1791–1804.

Angold PG, Sadler JP, Hill MO, Pullin A, Rushton S, Austin K, Small E, Wood B, Wadsworth R, Sanderson R, Thompson K 2006. Biodiversity in urban habitat patches. Science of the Total Environment 360: 196–204.

Arnold TW 2010. Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management 74: 1175–1178.

Aronson, MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA, Warren PS, Williams NSG, Cilliers S, Clarkson B, Dobbs C, Dolan R, Hedblom M, Klotz S, Kooijmans JL, Kühn I, MacGregor-Fors I, McDonnell M, Mörtberg U, Pyšek P, Siebert S, Sushinsky J, Werner P, Winter M 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proceedings of the Royal Society B: Biological Sciences 281: 20133330.

Borchers DL, Efford MG 2008. Spatially explicit maximum likelihood methods for capture– recapture studies. Biometrics 64: 377–385.

Braczkowski AR, Balme GA, Dickman A, Fattebert J, Johnson P, Dickerson T, Macdonald DW, Hunter L 2016. Scent lure effect on camera-trap based leopard density estimates. PLOS ONE 11: e0151033.

Burnham KP, Anderson DR 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd ed. New York, Springer. 512 p.

Caryl FM, Thomson K, van der Ree R 2013. Permeability of the urban matrix to arboreal gliding mammals: Sugar gliders in Melbourne, Australia. Austral Ecology 38: 609–616.

Carthew SM, Yáñez BM, Ruykys L 2015. Straddling the divide: den use by brushtail possums (*Trichosurus vulpecula*) in urban parklands. Urban Ecosystems 18: 525–538.

Chace JF, Walsh JJ 2006. Urban effects on native avifauna: a review. Landscape and Urban Planning 74: 46–69.

Clout MN 1977. The ecology of the possum (*Trichosurus vulpecula* Kerr) in *Pinus radiata* plantations. Unpublished PhD Thesis, University of Auckland, Auckland, New Zealand.

Clout MN 2006. Keystone aliens? The multiple impacts of brushtail possums. In: Allen RB, Lee WG eds. Biological Invasions in New Zealand. Berlin, Springer. Pp. 265–279.

Clout MN, Gaze PD 1984. Brushtail possums (*Trichosurus vulpecula* Kerr) in a New Zealand beech (*Nothofagus*) forest. New Zealand Journal of Ecology 7: 147–155.

Cowan PE 2005. Brushtail possum. In: King CM ed. The Handbook of New Zealand Mammals. Melbourne, Oxford University Press. Pp. 56–80.

Dearborn DC, Kark S 2010. Motivations for conserving urban biodiversity. Conservation Biology 24: 432–440.

Dice LR 1938. Some census methods for mammals. The Journal of Wildlife Management 2: 119– 130.

Distiller G, Borchers DL 2015. A spatially explicit capture-recapture estimator for single-catch traps. Ecology and Evolution 5: 5075–5087.

Duncan RP, Holland EP, Pech RP, Barron M, Nugent G, Parkes JP 2011. The relationship between possum density and browse damage on kamahi in New Zealand forests. Austral Ecology 36: 858–869.

Dunnet GM 1964. A field study of local populations of the brush-tailed possum *Trichosurus vulpecula* in eastern Australia. Proceedings of the Zoological Society of London 142: 665–695.

Efford MG 2000. Possum density, population structure, and dynamics. In Montague TL ed. The brushtail possum: Biology, impact and management of an introduced marsupial. Lincoln, Manaaki Whenua Press. Pp. 47–61.

Efford MG 2004. Density estimation in live-trapping studies. Oikos 106: 598–610.

Efford MG 2019. secr: spatially explicit capture-recapture models. R package version 3.5.2.

Efford MG, Cowan PE 2004. Long-term population trend of the brushtail possums *Trichosurus vulpecula* in the Orongorongo Valley, New Zealand. In: Goldingay RL, Jackson SM eds. The biology of Australian possums and gliders. Chipping Norton, Surrey Beatty & Sons. Pp. 471–483.

Efford MG, Warburton B, Coleman MC, Barker RJ 2005. A field test of two methods for density estimation. Wildlife Society Bulletin 33: 731–738.

Eymann, JD, Cooper W, Herbert CA 2013. Brushtail possums (*Trichosurus vulpecula*) in metropolitan Sydney: population biology and response to Suprelorin contraceptive implants. Australian Journal of Zoology 61 :78–86.

Foster RJ, Harmsen BJ 2012. A critique of density estimation from camera-trap data. The Journal of Wildlife Management 76: 224–236.

Freeman C, Buck O 2003. Development of an ecological mapping methodology for urban areas in New Zealand. Landscape and Urban Planning 63: 161–173.

Gallo T, Fidino M, Lehrer EW, Magle SB 2017. Mammal diversity and metacommunity dynamics in urban green spaces: implications for urban wildlife conservation. Ecological Applications 27: 2330–2341.

Glen AS, Byrom AE, Pech RP, Cruz J, Schwab A, Sweetapple PJ, Yockney I, Nugent G, Coleman M, and Whitford J 2012. Ecology of brushtail possums in a New Zealand dryland ecosystem. New Zealand Journal of Ecology 36: 29–37.

Harper MJ 2005. Home range and den use of common brushtail possums (*Trichosurus vulpecula*) in urban forest remnants. Wildlife Research 32: 681–687.

Harper MJ, McCarthy MA, Ree RVD 2008. Resources at the landscape scale influence possum abundance. Austral Ecology 33: 243–252.

van Heezik Y, Smyth A, Mathieu R 2008. Diversity of native and exotic birds across an urban gradient in a New Zealand city. Landscape and Urban Planning 87: 223–232.

Hocking GJ 1981. The population ecology of the brush-tailed possum, *Trichosurus vulpecula* (Kerr) in Tasmania. Unpublished MSc thesis, University of Tasmania, Tasmania, Australia.

Holland EP, Pech RP, Ruscoe WA, Parkes JP, Nugent G, Duncan RP 2013. Thresholds in plant–herbivore interactions: predicting plant mortality due to herbivore browse damage. Oecologia 172: 751–766.

Hooker MJ, Laufenberg JS, Ashley AK, Sylvest JT, Chamberlain MJ 2015. Abundance and density estimation of the American black bear population in central Georgia. Ursus 26: 107–115.

How RA 1972. The ecology and management of *Trichosurus* species (Marsupialia) in New South Wales. Unpublished PhD thesis, University of New England, NSW, Australia.

How RA, Hillcox SJ 2000. Brushtail possum, *Trichosurus vulpecula*, populations in southwestern Australia: demography, diet and conservation status. Wildlife Research 27: 81–89.

Hurvich CM, Tsai CL 1989. Regression and time series model selection in small samples. Biometrika 76: 297–307.

Isaac JL, Johnson CN 2003. Sexual dimorphism and synchrony of breeding: variation in polygyny potential among populations in the common brushtail possum, *Trichosurus vulpecula*. Behavioral Ecology 14: 818–822.

Lowry H, Lill A, Wong BBM 2011. Tolerance of auditory disturbance by an avian urban adapter, the noisy miner. Ethology 117: 490–497.

Lowry H, Lill A, Wong BBM 2013. Behavioural responses of wildlife to urban environments. Biological Reviews 88: 537–549.

Lustig A, James A, Anderson D, Plank M 2019. Pest control at a regional scale: identifying key criteria using a spatially explicit, agent-based model. Journal of Applied Ecology 56: 1515–1527.

le Mar K, McArthur C 2005. Habitat selection by common brushtail possums in a patchy eucalypt-forestry environment. Australian Mammalogy 27: 119–127.

Mathieu R, Freeman C, Aryal J 2007. Mapping private gardens in urban areas using object-oriented techniques and very high-resolution satellite imagery. Landscape and Urban Planning 81: 179–192.

Matthews A, Lunney D, Waples K, Hardy J 2004. Brushtail possums: "champion of the suburbs" or "Our tormentors". In: Lunney D, Burgin S eds. Urban Wildlife: More than meets the eye. Mosman NSW, Royal Zoological Society of New South Wales. Pp. 159–168.

McDonnell MJ, Pickett ST, Groffman P, Bohlen P, Pouyat RV, Zipperer WC, Parmelee RW, Carreiro MM, Medley K 2008. Ecosystem processes along an urban-to-rural gradient. In: Marzluff JM, Shulenberger E, Endlicher W, Alberti M, Bradley G, Ryan C, Simon U, ZumBrunnen C eds. Urban ecology. Boston, Springer. Pp. 299-313.

McKinney ML 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127: 247–260.

Montague T, Warburton B 2000. Non-toxic techniques for possum control. In: Montague TL ed. The brushtail possum: Biology, impact and management of an introduced marsupial. Lincoln, Manaaki Whenua Press. Pp. 164–174.

Mörtberg UM 2001. Resident bird species in urban forest remnants; landscape and habitat perspectives. Landscape Ecology 16: 193–203.

Nugent G, Whitford J, Sweetapple P, Duncan R, Holland P 2010. Effect of one-hit control on the density of possums (*Trichosurus vulpecula*) and their impacts on native forest. Science for Conservation 304. Wellington, Department of Conservation. 68 p.

Nugent G, Warburton B, Thomson C, Sweetapple P, Ruscoe WA 2011. Effect of prefeeding, sowing rate and sowing pattern on efficacy of aerial 1080 poisoning of small mammal pests in New Zealand. Wildlife Research 38: 249–259.

Otis DL, Burnham KP, White GC, Anderson DR 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62: 3–135.

Parmenter RR, Yates TL, Anderson DR, Burnham KP, Dunnum JL, Franklin AB, Friggens MT, Lubow BC, Miller M, Olson GS, Parmenter CA, Pollard J, Rexstad E, Shenk TM, Stanley TR, White GC 2003. Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. Ecological Monographs 73: 1–26.

Payton IJ 2000. Damage to native forests. In: Montague TL ed. The brushtail possum: Biology, impact and management of an introduced marsupial. Lincoln, Manaaki Whenua

Press. Pp. 111–125.
Pech R, Byrom A, Anderson D, Thomson C, Coleman M 2010. The effect of poisoned and notional vaccinated buffers on possum (*Trichosurus vulpecula*) movements: minimising the risk of bovine tuberculosis spread from forest to farmland. Wildlife Research 37: 283–292.
Pickett KN, Hik DS, Newsome AE, Pech RP 2005. The influence of predation risk on foraging behaviour of brushtail possums in Australian woodlands. Wildlife Research 32: 121– 130.
QGIS Development Team 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project.
R Core Team 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
Richardson KS, Rouco C, Jewell C, French NP, Buddle BM, Tompkins DM 2017. Investigating brushtail possum (*Trichosurus vulpecula*) home-range size determinants in a New Zealand native forest. Wildlife Research 44: 316–323.
Rouco C, Norbury GL, Smith J, Byrom AE, Petch RP 2013. Population density estimates of brushtail possums (*Trichosurus vulpecula*) in dry grassland in New Zealand. New Zealand Journal of Ecology 37: 12–17.
Rose AB, Pekelharing CJ, Platt KH 1992. Magnitude of canopy dieback and implications for conservation of southern rata-kamahi (*Metrosideros umbellata-Weinmannia racemosa*) forests, central Westland, New Zealand. New Zealand Journal of Ecology 16: 23–32.
Royle JA, Young KV 2008. A hierarchical model for spatial capture–recapture data. Ecology 89: 2281–2289.
Russell JC, Innes JG, Brown PH, Byrom AE 2015. Predator-free New Zealand: conservation country. BioScience 65: 520–525.
Russell JC, Stanley MC 2018. An overview of introduced predator management in inhabited landscapes. Pacific Conservation Biology 24: 371–378.
Sadlier R 2000. Evidence of possums as predators of native animals. In: Montague TL ed. The brushtail possum: Biology, impact and management of an introduced marsupial. Lincoln, Manaaki Whenua Press. Pp. 126–131.
Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH 2010. Invasion, competition, and biodiversity loss in urban ecosystems. BioScience 60: 199–208.
Shepherd JD, Gillingham S, Heuer T, Barron MC, Byrom AE, Pech RP 2018. Multiscale dynamic maps for the management of invading and established wildlife populations: brushtail possums in New Zealand. Wildlife Research 45: 336–343.
Soga M, Gaston KJ 2016. Extinction of experience: the loss of human–nature interactions. Frontiers in Ecology and the Environment 14: 94–101.
Statham M, Statham H 1997. Movements and habits of brushtail possums (*Trichosurus vulpecula* Kerr) in an urban area. Wildlife Research 24: 715–726.
Sweetapple PJ 2008. Spatial variation in impacts of brushtail possums on two Loranthaceous mistletoe species. New Zealand Journal of Ecology 32: 177–185.
Warburton BP, Cowan P, Shepherd J 2009. How many possums are now in New Zealand following control and how many would there be without it? Manaaki Whenua Contract Report LC0910/060. Lincoln, Manaaki Whenua – Landcare Research. 23 p.
Whyte BI, Ross JG, Blackie HM 2013. Differences in brushtail possum home-range characteristics among sites of varying habitat and population density. Wildlife Research 40: 537–544.
Wilson DJ, Efford MG, Brown SJ, Williamson JF, McElrea GJ 2007. Estimating density of ship rats in New Zealand forests by capture-mark-recapture trapping. New Zealand Journal of Ecology 31: 47–59.
Woolley CK, Hartley S, Hitchmough RA, Innes JG, van Heezik Y, Wilson DJ, Nelson NJ 2019. Reviewing the past, present and potential lizard faunas of New Zealand cities. Landscape and Urban Planning 192: 103647.

Received: 17 June 2020; accepted: 11 February 2021
Editorial board member: Tom Etherington