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RESEARCH

Home range overlaps of the brushtail possum (*Trichosurus vulpecula*): implications for disease transmission

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Abstract

Understanding how bovine tuberculosis (TB) is maintained in wildlife reservoirs is critical for the management of this disease impacting cattle in many countries. For the primary wildlife reservoir of the disease in New Zealand, the brushtail possum (*Trichosurus vulpecula*), transmission of this contagious bacterial disease among possums is often assumed to be linked to home range overlap. Identifying drivers of possum home range, and home range overlap between individuals, is thus important for informing wildlife reservoir TB management in New Zealand. We monitored four sub-populations of free-living possums in New Zealand native forests during 10 consecutive months using live trapping, to give the first direct insight into how the frequency and area of overlaps alters with density, sex and age. A total of 832 individuals were captured (average 9.3, range from 1 to 40 captures per animal with a median value of 7) and 35,820 home range overlaps were recorded. Both the number and area of overlaps were significantly associated with age class, with 66.6% of overlaps occurring between adults, 30% between adults and juveniles, and only 3.4% between juveniles. Overall, adult males showed significantly higher numbers of overlaps than expected, while adult and juvenile females showed significantly lower numbers of overlaps than expected and no differences were observed in juvenile males. In addition, males exhibited more and larger overlaps than females. The number and size of overlaps per individual decreased with increasing local population density. Understanding shared areas of activity among individuals can provide insights into the interactions occurring and potential pathways for diseases transmitted by contact such as TB. These results can inform to develop effective strategies for the control of diseases carried and dispersed by possums.

Keywords Epidemiology · Disease control · Population structure · Possum behaviour · Bovine tuberculosis · Wildlife management

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Introduction

Wildlife studies estimating animal home range characteristics and behaviour are a valuable source of information in ecology, wildlife management and epidemiology (Lugton 1997; Nugent et al. 2013; Tobajas et al. 2020). For example, numerous studies attribute the transmission of contagious infectious diseases to contact or close proximity among individuals (Whyte et al. 2013; Craft 2015; Podgórski et al. 2018), indicating that home range dynamics likely play a key role in determining intra-specific transmission. One such disease is bovine tuberculosis (TB), for which the causative agent, *Mycobacterium bovis*, can be transmitted by direct contact between individuals (Buddle et al. 1994; Gortázar et al. 2015) and likely also via environmental contamination. Although *M. bovis* is fragile (see Morris et al.

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1994), experiments have shown that it may persist in the environment for months (Tanner and Michel 1999; Fine et al. 2011). Thus, shared occupation of the same area is likely another key pathway by which animals are infected (Porphyre et al. 2011; Barasona et al. 2017).

For solitary species that tend not to undergo large spatial movements, home range overlaps with infected individuals are one of the most likely determinants of both individual encounters and co-occupation, and hence contagious disease transmission (Hirsch et al. 2013; Rouco et al. 2018). This is the basis of density-dependent transmission functions used in epidemiological models, where the force of infection increases linearly with population density (Morris et al. 1994; Begon et al. 2002). However, disease persistence is frequently observed at low densities (e.g. May and Anderson 1979; Swinton et al. 2002; Moran et al. 2021), at which such transmission functions predict that 'fade-out' should occur, and such persistence can cause disease management by suppressing populations to fail.

The primary wildlife reservoir of TB in New Zealand is the brushtail possum *(Trichosurus vulpecula)*, in which TB has persisted in some sub-populations despite management of its populations (Nugent 2011). Possums are generally considered solitary (Crawley 1973; Clout and Efford 1984; Nugent et al. 2000), but can come into proximity and contact through both breeding (Bell 1981; Cowan 1993; Ramsey et al. 2002) and communal denning (Cowan 1989; Caley et al. 1998). Previous studies have demonstrated how possum home range size, in general, is negatively correlated with sub-population density (Bell 1981; Efford et al. 2016; Rouco et al. 2017). Although this non-linearity is accounted for in modelling and by management (Rouco and Norbury 2015; Yockney et al. 2015; Anderson et al. 2022), it is based on an assumed relationship between possum density and home range size, and both the frequency and extent of home range overlaps. How the frequency and extent of home range overlaps alter with density and home range size has yet to be directly investigated, with such information potentially allowing improved model predictions for management. Should there be non-linearities between density and the overlapping of home ranges that are not captured solely by density and home range size, transmission potential may still be underestimated.

We addressed this knowledge gap in a study of four sub-populations of free-living possums, monitoring the frequency and area of home range overlaps within each sub-population in relation to local population density and both possum age class and sex, all of which are known determinants of possum home range size (Whyte et al. 2013; Richardson et al. 2017). Understanding how animals utilize their habitat and coexist with one another is crucial for comprehending disease transmission, its spread, and persistence within populations. Moreover, this newfound knowledge may lead to improvements in current pest control management strategies.

Materials and methods

Study site

The study site was a designated research area in the Orongorongo Valley on the North Island of New Zealand (41°21'S, 174°58'E). The valley is orientated north to south, runs between steep ridges rising to 670 m above sea level, and contains mixed beech/podocarp forest that supports high possum densities (>4 individuals/ha) (Efford and Cowan 2004; Richardson et al. 2017; Margetts et al. 2020).

Data collection

Possums were captured during monthly trapping sessions from March to December 2012, from the start of the Austral autumn through to early summer. The trapping period includes the peak of possum breeding season (April–June) at the study site (Fletcher and Selwood 2000). Each trapping session consisted of four consecutive trap nights, with traps being checked and re-baited each day. The trapping area consisted in four square trapping grids (A, B, C, and D) on the east ridge of the Orongorongo Valley, each made up of 100 traps at 40 m spacing covering approximately 16 ha. The distance between study grids was approximately 650 m. Mean possum density (SE) was 4.87 (0.19), 6.92 (0.29), 4.81 (0.21) and 4.20 (0.19) ha^{-1} for grids A–D, respectively (Richardson et al. 2017).

Possums were captured in Grieve wire cage traps (60 × 26 × 28 cm) with spring-assisted folding doors triggered by a pendulum bait hook (Buddle et al. 1994; Warburton et al. 2000). The bait used was apple with flour mixed with icing sugar and cinnamon essence. Upon initial capture, individuals were anaesthetized by intra-muscular injection of Zoletil 100® (Virbac New Zealand Ltd, Auckland, New Zealand; Morgan et al. 2012), tagged in both ears with unique numbered tags (National Band & Tag Co. size 3, Kentucky, USA), and had their sex and juvenile/adult status recorded before being released at the trap site where they were caught. Possums were classified as belonging to either a 'juvenile cohort' or an 'adult cohort' based on the developmental stage of the pouch/testes and tooth wear at initial capture (Corner et al. 2003; Ramsey et al. 2006). We justified leaving juvenile possums listed within the juvenile cohort throughout the yearlong study as these possums likely still lacked the sexual maturity to behave as adult possums before the next trapping season.

Individual home range size and home range overlap estimation

All trap locations were recorded in the field as Universal Transverse Mercator coordinates (UTM) using a Garmin-12 Global Positioning System (GPS) portable receiver. The 100% Minimum Convex Polygon method (MCP; Mohr 1947) was used to estimate home range sizes on an individual basis across the full 10 months of data. This was implemented in the program ArcView 3.2 (Environmental Systems Research Institute, California, USA), with a buffer area set as half the distance between traps (20 m). MCP estimates were obtained for all animals that were trapped at least five times during the ten months. Whether the home range of each possum on each grid overlapped with that of each other possum, and the extent of such overlaps when they occurred, were then calculated based on the geo-located MCPs, also using ArcView 3.2. This resulted in two types of outcome variable: one at the possum level (i.e. the number of home ranges overlapped for each possum) and one at the level of the overlap (i.e. the area of overlap for each pair of possums or dyad).

Statistical analysis

To investigate the effects of sex, age, and grid on the number of home range overlaps, we used generalized linear models (GLM) with Poisson distribution and log link. The explanatory variables considered for this outcome were the possums' sex, age, grid and their interactions. If significant differences between study sites were found, a pairwise post hoc comparison between factors was performed using Tukey's test. In addition, to assess the concordance between the number of possums overlapping in different age and sex categories and the expected distribution of possum individuals across these categories within the possum population, we conducted a two-tailed Chi-square test (χ^2) at both the total population and grid level. The expected distribution was calculated based on the demographic structure of the possum population in terms of sex and age categories. A significant deviation of the observed distribution of possum overlaps from the expected population structure ($p < 0.05$) would suggest notable differences in the overlap among specific age and sex combinations. Conversely, if the proportion of possum overlap resembled the population structure, it would indicate that the overlap occurrences are random with respect to the age and sex distribution within the possum population.

To test the effects of sex, age, and grid on the area of home range overlap, we used linear mixed models (LMM) with normal distribution and identity link function. The explanatory variables considered in the model were the sex and age combinations of the dyad, the grid where the overlaps occurred, and the interaction between age and sex and with the grid. For sex, the combinations of sexes for each pair were male/male (MM), male/female (MF) or female/female (FF) dyads. For age, the combinations were adult/adult (AA), adult/juvenile (AJ) or juvenile/juvenile (JJ) dyads. We included the possum-level effect in our model as a multi-membership random effect structure using the "lmerMultiMember" pakage in R 4.4.0 (R Core Team 2024), accounting for the identity of both possums in the pair. If significant differences were found, pairwise post hoc comparisons between factors was performed using Tukey's test. Log transformations were applied to home range estimators to meet the normality assumptions of the models. All the models were performed using the R packages "lme4" and "emmeans" in R 4.4.0 (R Core Team 2024). We checked for collinearity, marginal distribution, and heteroscedasticity of residuals using the Shapiro–Wilk normality test and Q–Q plots to ensure normality, and visual checks to meet homoscedasticity assumptions.

Results

Number of overlaps

Among the 832 individuals (average 9.3, range 1–40 captures per animal) monitored across the four trapping grids, 35,820 home range overlaps occurred, with 43.05 ± 24.17 overlaps per individual (Table 1). Of the total recorded

Table 1 Overall data of the captured possums and home range overlaps (mean ± SE) in the trapping grids from the research area in the Orongorongo Valley on the North Island of New Zealand

	Grid			
	A	B	C	D
Possum density (individuals/ha)	4.87 (0.19)	6.92 (0.29)	4.81 (0.21)	4.20 (0.19)
Captured possums	214	240	185	193
Adult males	82	73	67	68
Adult females	98	113	70	89
Juvenile males	15	30	29	22
Juvenile females	19	24	19	14
Total home range overlaps	9,704	8,216	10,056	7,844
Mean possum home range overlaps	45.35 (1.60)	34.23 (1.33)	54.36 (1.98)	40.64 (1.56)
Mean possum overlap area (ha)	0.29 (0.004)	0.18 (0.002)	0.35 (0.005)	0.34 (0.005)

home range overlaps, 66.6% occurred between adult possums, while only 30% of overlaps were between adults and juveniles, and only 3.4% were between juveniles (Fig. 1).

There were significant relationships between the number of home range overlaps shared between possums and sex ($\chi^2=27.9$, df=1, $P<0.001$), age ($\chi^2=14.3$, df=1, $P<0.001$) and grid ($\chi^2=82.4$, df=3, $P<0.001$). However, significant interactions between sex and age, grid and sex, and between grid, sex and age were not found. Overall, males had higher numbers of overlaps than females, both adults and juveniles, but significant differences were only found between adult males and both adult and juveniles females ($P<0.001$) (Fig. 1). Similarly, adult males had higher numbers of home range overlaps than juvenile males ($P=0.01$) (Fig. 1). In contrast, no significant differences were found between adult females and juvenile males and females ($P>0.05$), nor between juvenile females and juvenile males ($P=0.22$) (Fig. 1). With regards to grid, there were significantly fewer home range overlaps on the grid with higher possum density (grid B) than on other grids ($P<0.05$), and significantly higher numbers of overlaps on grid C ($P<0.01$) than on the other grids (A and D) with similar possum densities (Fig. 1). No differences in numbers of overlaps was observed between the grid A and D ($P=0.21$).

Overall, the number of home range overlaps differed with possum population structure, based on total numbers of possums and overlaps ($\chi^2=478.26$, df=4, $P<0.001$) and in each grid (A: $\chi^2=269.34$, df=4, $P<0.001$; B: $\chi^2=383.36$, df=4, $P<0.001$; C: $\chi^2=42.8$, df=4, $P<0.001$; D: $\chi^2=262.44$, df=4, $P<0.001$). Adult males had higher numbers of overlaps than expected in all grids ($P<0.001$), while juvenile males showed no differences to the expected numbers of overlaps in all grids ($P>0.1$). In the case of females, the numbers of overlaps were lower than expected in all grids ($P<0.001$), less in grid C for adult females ($P=0.33$), and less in grid D for juvenile females ($P=0.12$).

Area of overlaps

When possums home ranges overlapped, the shared area between individuals depended on both sex and age ($\chi^2=26.7$, df=2, $P<0.001$ and $\chi^2=18.9$, df=2, $P<0.001$, respectively). Additionally, the models revealed significant

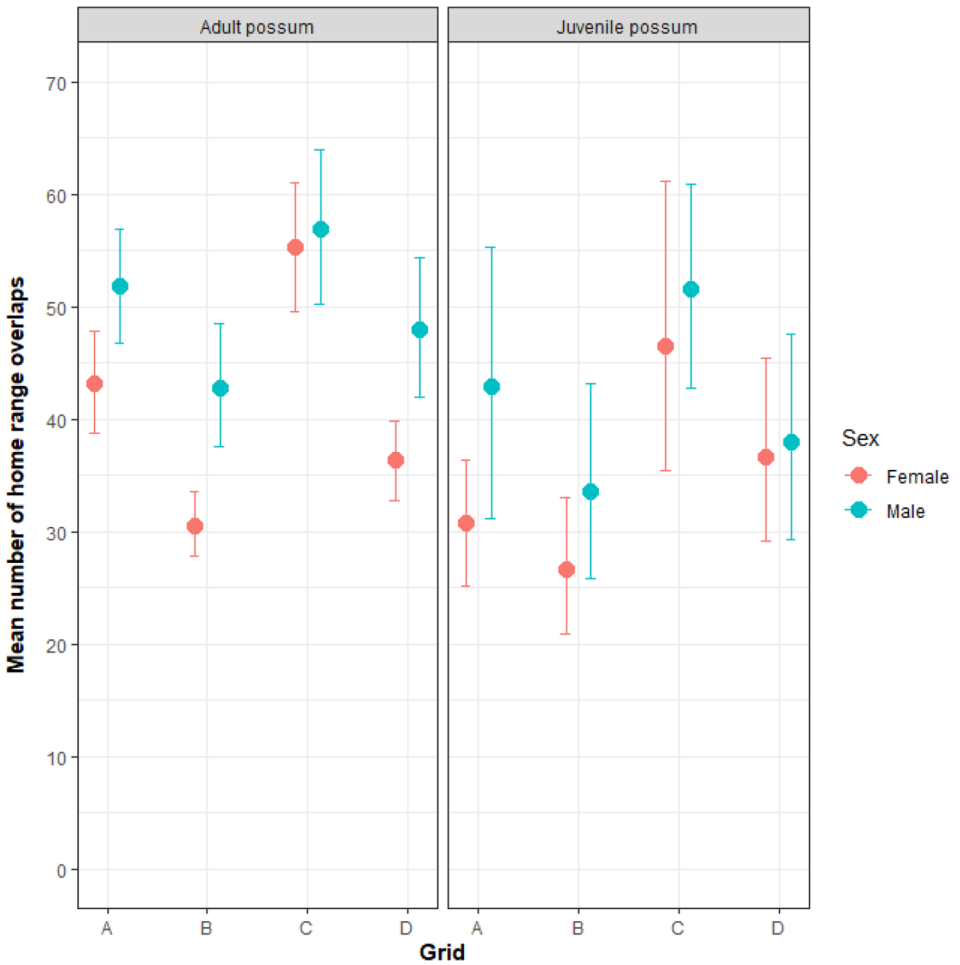

Fig. 1 Mean number (±95% CI) of home range overlaps across all four grids broken down by sex and age of possums with overlapping boundaries

differences between the grids ($\chi^2 = 34.9$, df = 3, $P < 0.001$). Significant interactions were found between sex and age ($\chi^2 = 12.2$, df = 4, $P = 0.016$) and age and grid ($\chi^2 = 20.1$, df = 6, $P = 0.002$), but not between sex and grid ($\chi^2 = 3.2$, df = 6, $P = 0.78$). Adult male possums had larger overlap areas than adult and juvenile females ($P < 0.01$), and also than juvenile male possums ($P < 0.01$) (Fig. 2). Conversely, no significant differences were found between the overlap areas of adult and juvenile female possums ($P > 0.05$), nor between juvenile male possums and juvenile females (Fig. 2).

There were also significant differences between the grids in the area of home range overlaps ($\chi^2 = 34.9$, df = 3, $P < 0.001$). The post hoc analysis indicates significant differences between all the grids ($P < 0.05$) except between grids C and D ($P > 0.05$), which had the largest possum home range overlap areas (Table 1; Figs. 3 and 4). Interestingly, these grids had the lowest possum densities. In contrast, grid B had the smallest home range overlap areas, followed by grid A (Table 1; Figs. 3 and 4), which had the largest possum densities. As shown by the lack of interaction effect between sex and grid ($\chi^2 = 3.2$, df = 6, $P = 0.78$), male possums had greater overlap areas, followed by females and juveniles (Fig. 3). There were also differences in overlap areas between grids as a function of age ($\chi^2 = 20.1$, df = 6, $P = 0.002$), with adult possums having larger areas of overlap with other adults than with juvenile possums (Fig. 4). However, this pattern was not apparent in grid B, which had the highest possum densities (Fig. 4).

Discussion

The aim of this study was to investigate the determinants of possum home range overlap by assessing which possums share overlaps and to what extent the overlaps occur. Our results revealed that males had generally more, and larger, home range overlaps with other possums than females did (Figs. 1, 2 and 3). When examining the dyads, the overlaps between males were the largest while the overlaps between females were the smallest with male/female home range overlaps being of intermediate size (Fig. 3). These results are in accordance with other studies (Crawley 1973; Paterson et al. 1995; Efford et al. 2000).

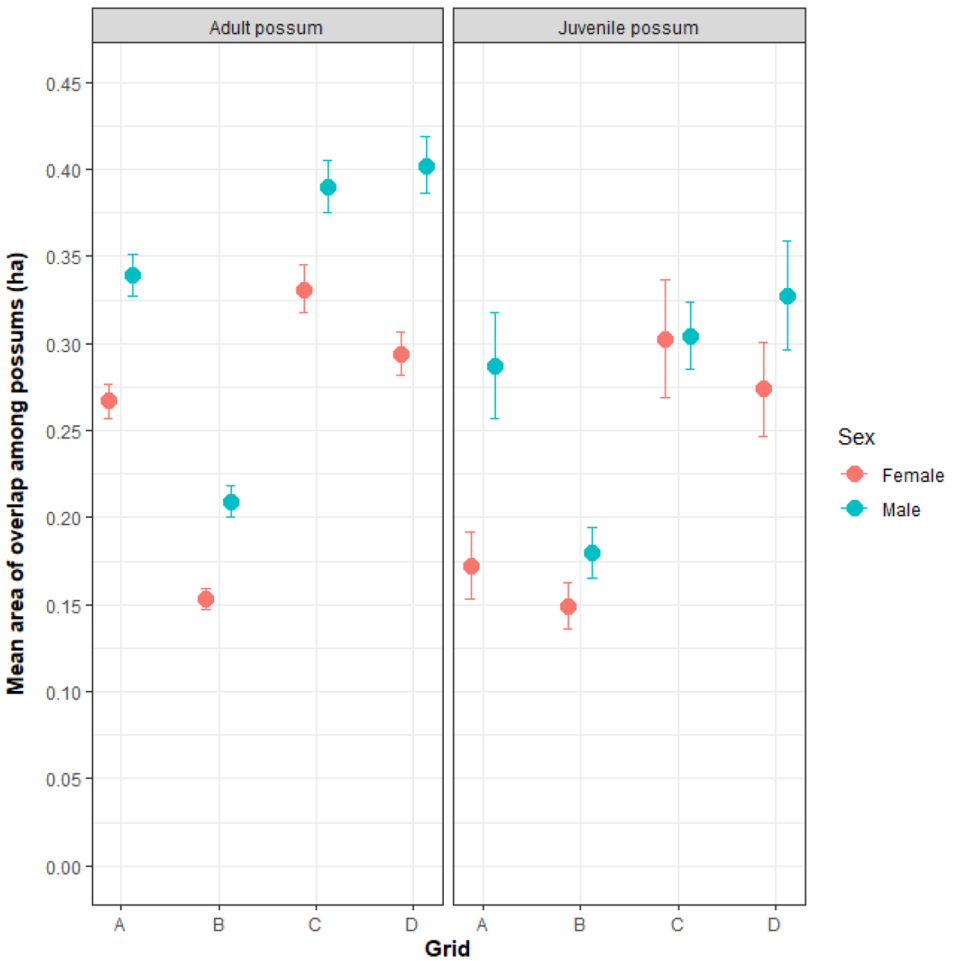

Fig. 2 Mean (±95% CI) of the area of home range overlap shared among possums separated by sex and age cohorts across all four grids

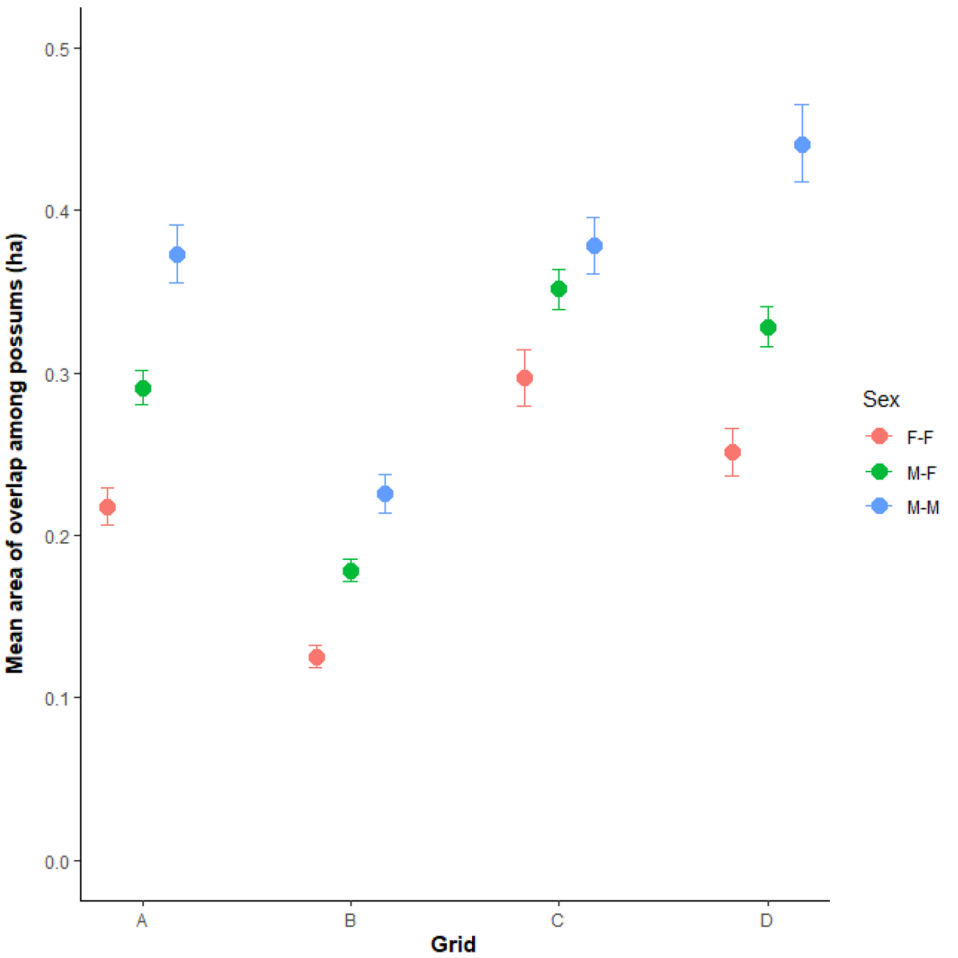

Fig. 3 Mean (±95% CI) of the area of home range overlaps shared among pairs of male/male (M-M), male/female (M-F) and female/female (F-F) across all four grids

In a previous study, Richardson et al. (2017) found that juvenile possums did not necessarily have smaller home ranges than adult possums, however this study shows they do have fewer and smaller home range overlaps with other possums. This reinforces previous findings (Blackie et al. 2011), and is likely due to behavioural differences, with juvenile possums perhaps showing a greater level of avoidance behaviour with respect to other individual possums than adult possums have, or adult possums being less tolerant of juveniles in their home ranges than they are of other adults. In addition to these intrinsic drivers of possum home range overlap, extrinsic effects were also apparent through the significant grid effect. Some authors had revealed the negative relationship between abundance and possum's home range size (Whyte et al. 2013; Efford et al. 2016; Rouco et al. 2017; Margetts et al. 2020). Here, home range overlaps were fewer (per possum) and smaller when they occurred on Grid B, which had higher density than the other grids, resulting in smaller home ranges (Table 1). Ours and previous research seems to indicate the existence of density dependence in the home range size and overlaps, which can be explained by several ecological and behavioural factors. In high-density populations, resources such as food and space are limited and highly contested. This leads to the establishment of smaller, more exclusive territories as individuals aim to secure sufficient resources while minimizing direct competition and aggressive interactions (Rouco et al. 2017; Margetts et al. 2020). Consequently, home range overlaps are less frequent and smaller in size because individuals defend their territories more rigorously. Conversely, in lower-density populations that might be below carrying capacity, resources are more abundant and less contested per individual (Rouco et al. 2017). This allows possums to expand their home ranges without the need for aggressive defence, leading to an increase in both the number and size of home range overlaps (Whyte et al. 2013; Richardson et al. 2017). Individuals can move more freely across larger areas in search of preferential resources without encountering significant resistance from others, except in the territorial core areas (Day et al. 2000; Margetts et al. 2020). Furthermore, in low-density populations, the need to travel further to find mates and resources can also contribute to increasing the number of home range overlaps, which increases the visits and use of neighbours dens (Whyte et al.

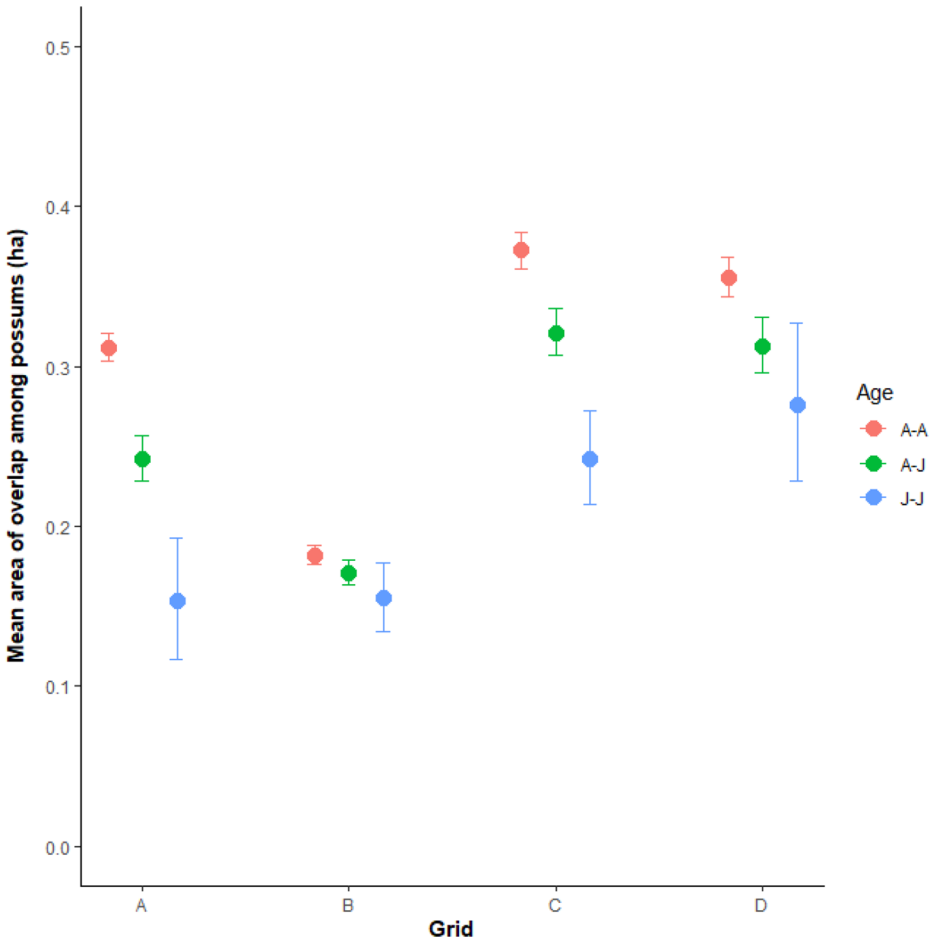

Fig. 4 Mean (±95% CI) of the area of home range overlap shared among pairs of adult/adult (A-A), adult/juvenile (A-J) and juvenile/juvenile (J-J) across all four grids

2013). This expansion and increased overlap of home ranges can be seen as a strategy to maximize access to dispersed resources and increase the likelihood of encounters with potential mates. However, other factors related to habitat characteristics such as food and den availability might also explain some of these differences between grids (Harper et al. 2008; Rouco et al. 2013; Whyte et al. 2013; Richardson et al. 2017). Future research should explore whether there is a density threshold below which home range overlap size and number starts to decline, which would provide further insight into the relationship between habitat quality, population density and spatial behaviour in possums.

Our findings have several key implications for understanding the persistence and spread of TB in possums, and potentially also its management. First, the smaller number and size of juvenile than adult possum home range overlaps (irrespective of population density), suggests that they likely find themselves less frequently in proximity with potentially TB infected individuals. Regardless of the actual mechanism of transmission, be it through environmental contamination or actual contact (Nugent et al. 2015), this strongly suggests that they are at lower risk than adults of contracting the disease. This hypothesis is supported by the generally much lower rate of TB infection observed in juvenile than adult possums (Crawley 1973; Buddle et al. 1994; Zinsstag et al. 2006; Gortazar and Cowan 2013). Moreover, even if juvenile individuals do become infected (e.g., through contact with an infected mother), their home range overlaps with other possums are slightly less than those of adults. This suggests they might play a somewhat smaller role in disease transmission. However, it is likely that infected juvenile possums who survive and become adults will start to play a larger role in transmission.

Second, the larger number and size of home range overlaps (again, irrespective of population density) for adult male possums than for adult female possums (apparently driven simply by them having larger home range sizes; Richardson et al. 2017) indicate that this population subgroup may play a disproportionally larger role in TB disease dynamics (Rouco et al. 2018). Additionally, males are more likely than females to come into proximity with any infected individual in any neighbourhood. TB-infected males appear to live longer than infected females (Rouco et al. 2016), meaning infected adult males may come into proximity with

more susceptible individuals than infected adult females (Rouco et al. 2018). In these ways, this population subgroup may be acting as a disease 'superspreading' group (Lloyd-Smith et al. 2005; Matthews et al. 2006; Chase-Topping et al. 2008; Rouco et al. 2018).

Finally, the differences in possum home range parameters noted for the subpopulation on Grid B, at markedly higher population density than the other three subpopulations (Table 1), imply issues for TB management through population suppression (Ramsey et al. 2002; Margetts et al. 2020). If high density is indeed the driver of the observed overall smaller individual home ranges on Grid B, having fewer and smaller overlaps with other individuals (Table 1), then home range overlaps per individual will be both more and larger at lower density increasing the likelihood of disease transmission encounters with TB infected individuals. These phenomena could lead to non-linearity in the relationship between possum density and disease transmission rates (Ramsey et al. 2002; Porphyre et al. 2011), with infected individuals potentially being more likely to pass the infection on at lower density. This is inverse to the logic that the use of population suppression to control disease is based on.

The balance of these effects, and the potential for adult males to also drive TB transmission through their larger home ranges and social interactions (Rouco et al. 2018), will need to be further explored. Of critical importance to TB dynamics, will be ascertaining if and how the home range patterns documented here translate into actual contact/proximity rates between individuals. For the study of infectious disease dynamics in vertebrate wildlife in general, the evidence here for certain population groups potentially having larger roles in disease transmission than others, and the suggestion that per-capita opportunities for transmission may increase at low density rather than decrease due to home range behaviour effects (Porphyre et al. 2011), provides avenues of exploration in other systems where population control has failed to manage disease occurrence. Hence, among other factors such as management leaving higher-density patches where disease can persist, or not suppressing populations long enough for fade-out to occur, or transmission from other wildlife species, TB transmission among possums deviating from density-dependence is another factor potentially contributing to disease persistence.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Ethics approval All animal manipulations were conducted under permit 12/02/01 from the Landcare Research Animal Ethics Committee.

Competing interests The authors declare no competing interests.

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