Title: Brushtail possum (*Trichosurus vulpecula*) social interactions and their implications for bovine tuberculosis epidemiology

Short title: Possum social networks and TB

C. Rouco[1,2,*], C. Jewell[3]; K. S. Richardson[4,5]; N. P. French[4]; B. M. Buddle[5]; D. M. Tompkins[6]

[1] Manaaki Whenua Landcare Research, Dunedin, New Zealand

[2] Departamento de Zoología, Universidad de Córdoba, Spain

[3] CHICAS, Faculty of Health and Medicine, Lancaster University, Lancaster, England, United Kingdom

[4] [m]EpiLab, Hopkirk Research Institute, Massey University, Palmerston North, New Zealand

[5] AgResearch, Hopkirk Research Institute, Palmerston North, New Zealand

[6] Predator Free 2050 Ltd, Auckland, New Zealand

*Corresponding authors:

roucoc@landcareresearch.co.nz; c.rouco@gmail.es

Landcare Research, 764 Cumberland Street, Dunedin, New Zealand, 9016.

Phone +34 957 218 517

Present address: Departamento de Zoología, Campus de Rabanales, Universidad de Córdoba, 14071 Córdoba, Spain.

Abstract

The brushtail possum is the main reservoir of bovine tuberculosis in New Zealand. Its transmission among possums most likely occurs between individuals in close proximity and it generally tends to be higher in males than in females. This has conventionally been assumed due to greater infection rates of males, but recent work has raised the hypothesis that it may instead be driven by survival differences. Here we analyse social networks, built on data from wild possums collared with contact loggers inhabiting a native New Zealand forest, to investigate whether there is mechanistic support for higher male infection rates. Our results revealed that adult female possums were generally just as connected with adult male possums as other adult males are, with male-female connection patterns not being significantly different. This result suggest that the new 'survivorship' hypothesis for the sex bias is more likely than the conventional 'infection rate' hypothesis.

Keywords:

Mycobacterium bovis, Orongorongo Valley, social networks, vertebrate pest

Introduction

Brushtail possums (*Trichosurus vulpecula*) are medium sized (2 – 3 kg), nocturnal, arboreal marsupials native to Australia that were introduced to New Zealand in 1858 to establish a fur trade (Montague, 2000). They now occupy most of New Zealand with an estimated population size of 30 million (Nugent et al., 2015), and are the main wildlife reservoir for bovine tuberculosis (TB) in the country. Although three other wild mammal species are frequently infected with TB in New Zealand (ferrets, *Mustela furo*; feral deer, *Cervus elaphus*; feral pigs, *Sus scrofa*), they generally serve as 'spillover' hosts except for ferrets when they occur in high density (Nugent et al., 2015).

Disease transmission from infected possums is a major contributor to cattle herd TB infection (Nugent et al., 2000; Nugent et al., 2015). Its role as a reservoir species has been clearly demonstrated (Caley et al., 1999); management reduced infected cattle and deer herds in New Zealand by 96% from 1994 to 2014 mainly through possum population culling and movement control and test and slaughter of cattle and deer herds (Livingstone et al., 2015). TB prevalence in wild unmanaged possums tends to be highly variable both spatially among populations and temporally within them (Montague, 2000), but one relatively consistent characteristic is a sex bias with more males than females generally being infected (Lugton, 1997; Ramsey & Cowan, 2003). This has conventionally been assumed due to greater infection rates of males (Montague 2000).

The primary route by which possums become infected with *M. bovis* remains unclear but is most likely by direct transmission via the respiratory route (Coleman & Caley, 2000). Occasional

63 transmission may also occur by ingestion of infected material (or milk), percutaneous infection
64 of limbs through fighting, and via environmental contamination (Nugent et al., 2015). Although
65 *M. bovis* can survive for extended periods in dark enclosed places (e.g. dens), it is extremely
66 fragile in open well-lit environments (Morris et al., 1994). Additionally, other species may be in-
67 volved in the persistence of TB in the wild. Scavengers such as ferrets and pigs may become in-
68 fected after ingestion of *M. bovis*-infected tissue from the carcasses of infected possums (Cole-
69 man and Cooke 2001) acting as secondary reservoirs. Hence, although the pathway by which TB
70 transmission happens it is not completely clear, evidence strongly supports TB transmission
71 among possums occurring mostly between individuals in close proximity through behaviours
72 such as breeding, fighting and den sharing (Barlow, 1991; Nugent et al., 2015).
73
74 The inferred mechanism for greater TB infections rates of male possums is that the well docu-
75 mented larger home ranges of male than females (Efford et al., 2000; Yockney et al., 2013;
76 Rouco et al., 2017; Richardson et al., 2017) results in them encountering other possums more
77 frequently, and thus having higher probabilities of coming into close proximity to infected indi-
78 viduals (Montague, 2000). However, recent work has raised the hypothesis that it may instead be
79 driven by survival differences. With significantly greater survival rates of male versus female TB
80 infected free-living possums now documented (Rouco et al., 2016). Here we use social network
81 analysis to investigate whether there is similar mechanistic support for the 'infection rate' hy-
82 pothesis for the observed bias. Quantifying possum social networks is thus vital for understand-
83 ing TB dynamics. Such knowledge has proven invaluable for understanding the dynamics of
84 other infectious diseases (Buddle & Young, 2000; Matthews et al., 2009; Nugent et al., 2015),

85 including TB in Eurasian badgers (*Meles meles*; Weber et al., 2013). For possums, this infor-
86 mation is mostly unknown. While studies have focused on population characteristics such as
87 density (e.g. Buddle & Young, 2000; McCallum, 2009; Whyte et al., 2014; Nugent et al., 2015)
88 and home range size (e.g. Arthur et al., 2002; Whyte et al., 2014; Nugent et al., 2015; Richardson
89 et al., 2017), only few attempts have focused in determining social networks parameters in pos-
90 sums (Corner et al., 2003; Ji et al., 2005; James et al., 2017), yet it remains unclear which if any
91 of these factors influence possum interactions and the manner in which they do so.
92
93 Here we investigate the social interactions of possums in four subpopulations within the Orongo-
94 rongo Valley, a long-term study site for the research and management of TB in possums in New
95 Zealand (Tompkins et al., 2009) that supports high possum densities (Efford and Cowan, 2004).
96 TB prevalence in possums at the site is generally low (i.e. < 5%, Arthur et al., 2004), with no
97 clear seasonality and little or no apparent relationship between possum abundance and disease
98 prevalence (Coleman & Caley, 2000). For the 'infection rate' hypothesis of TB prevalence sex
99 bias to be supported, we expect males to have more connections in the social network than fe-
100 males simply due to their larger home ranges resulting in a higher probability of encountering
101 other individuals.
102
103 **Methods and materials**
104
105 *Ethics statement*
106 All animal manipulations were conducted under permit 12/02/01 from the Manaaki Whenua Ani-
107 mal Ethics Committee.

Study site

The study site was a designated 1200 ha 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.

Data were obtained from four square trapping grids or subpopulations (A, B, C, and D) on the east ridge of the Valley, with grids separated by approximately 650 m. Possum density (±SE) was 4.9(0.2), 6.9(0.3), 4.8(0.2), 4.2(0.2) possums/ha for grids A, B, C, and D, respectively (see Richardson et al., 2017). Each grid was made up of 100 traps at 40 m spacing covering approximately 13 ha. All trap locations were recorded in the field as Universal Transverse Mercator coordinates (UTM) using a Garmin-12 Global Positioning System (GPS) portable receiver. Possums were captured in Grieve wire cage traps (60 cm × 26 cm × 28 cm) set on the ground with spring-assisted folding doors triggered by a pendulum bait hook.

Data collection

Trapping was carried out at monthly intervals during the study period (April–September 2012), which included the breeding season (April–June; Fletcher & Selwood, 2000). Each session consisted of traps being opened and checked for four consecutive nights at each site (with sprung traps reset, and possums recaptured during a trapping session only identified and released). Traps were set and baited each morning with apple sprinkled with powdered sugar and flour lured with anise oil. When first captured, possums were anesthetized by intra-muscular injection of Zoletil 100® (Virbac New Zealand Ltd, Auckland, New Zealand) (Morgan et al., 2012), weighed to the

nearest 25 g, sexed, ear-tagged with a numbered metal tag on each ear (National Band & Tag Co. size 3, Kentucky, USA), and released at the point of capture. Individuals were identified as either adults or juveniles based on pouch/testes development (Ramsey et al. 2006).

During the initial capture months (i.e. April and May), up to 40 adult possums (20 male and 20 female) on each trapping grid were fitted with a Sirtrack™ (Havelock North, New Zealand) encounter proximity radio-collar (UHF communication). Collars were programmed to detect and record other collars within 1 m, with a separation time of one second (i.e. an interaction ended if the collars were more than 1 m apart for more than one second). On the first occasion in each subsequent monthly trapping session, each recaptured collared possum was anesthetized as before, had its collar information downloaded on-site via cable connection to a notebook computer, and was then released. Collars that did not function correctly were replaced. The proximity collars had a battery life of around six months, which determined our analytical time frame.

The data consisted of a separate dataset for each individual on a trapping grid, with each record in a dataset representing a contact between that individual and another individual at the same site. Each record contained the ID of the individual encountered, the time and date at which the encounter occurred, and the length of the encounter. In theory, every encounter should have been recorded twice (i.e. once in the dataset of each interacting individual); however, in practice, only 60% of the pairs had fully consistent records for both individuals. Inconsistent records are frequently generated by differing alignments of the proximity collars to one another. All contact records from sites B and D were useable. At sites A and C, 34% and 3% of the records respectively were discarded because they were either corrupt or because the encounter length was

longer than 1000 minutes. Not all possums with proximity loggers were caught and therefore they are not present in our data; the dependent variables in analyses conducted thus only have observations for the possums caught. There was no apparent association between possum characteristics and missing data; thus, this should not have introduced bias to the analyses conducted.

Within trapping grids there was a structural contact bias meaning that possums located near the centroid of each grid had a greater chance of contacting other collared possums than possums located on the perimeter of the grids. To control for this bias, the number of possums with overlapping home ranges to each contactor over the entire study period was included as an analysis variable where relevant. Home ranges were based on the GPS locations of the traps in which each individual was caught. Incremental area analysis (Kenward 2001) was used to determine the appropriate number of locations needed to correctly estimate home-range size; home ranges were considered fully revealed when animals were trapped at least 10 times (see Richardson et al., 2017). Individual home ranges were estimated using the 100% minimum convex polygon method (MCP), and the number of overlaps calculated from the geo-located MCPs (implemented in ArcView 3.2, Environmental Systems Research Institute, California, USA).

Network characteristics

All analyses were conducted in *R* version 3.4.0. (R Core Team 2017). Collar data was used to characterize the subpopulation network structure separately for possums on each of the four trapping grids. Network parameters included node degree, edge strength and betweenness (see Table 1 for definitions and references for these measures). To standardize data for cross-grid comparisons, relative values for node degree and betweenness were estimated (see Table 1 for notation

definitions and equations); i.e. relative degree centrality (RDc_i) and relative betweenness centrality for undirected networks (RBc_i) (Lugton, 1997). Edge strength does not need to be corrected for the size of the network, being the number of contacts between each pair of possums. Packages *Dplyr* (Wickman et al., 2017) and *Igraph* (Csardi & Nepusz, 2006) were used to set up a working database and to construct network graphs/webs for viewing the distribution of contacts between individuals. Spearman rank correlations were used to compare social network parameters and possums density per grid using the *cor()* function.

Determinants of connectivity

An exponential random graph model (ERGM; Robins et al., 2007; Silk & Fisher, 2017) was used to investigate whether connectivity between possums was associated with both possum sex and trapping grid, using packages *ergm* and *scoringRules* (Hunter et al., 2008). The number of contacts observed for each dyad (potentially interacting pair of individuals) was converted into a binary variable (1 if possums were "in contact", and 0 otherwise). A network edge was initially defined as existing between two possums if a 'contact cut-off' of at least one contact between them had been recorded. The presence of edges was then regressed onto the sex combination of the possum dyad, accounting for the grid-grouping effect, and the density of the network (measured as the number of geometrically-weighted edge-shared partners per dyad, with decay parameter jointly estimated). The number of overlapping home-ranges for each possum was also included to account for the inherent downward bias in node degree occurring in possums close to the boundaries of our study grids.

The definition of our binary network structure was explored, with edge definition cut-offs from 1 up to 20 recorded contacts being modelled. Model fit (see Suppl. Mat.) in each case was quantified by calculating a continuous rank probability score (CRPS) to compare the observed distributions of node degree and edge shared partners (other nodes linked to both nodes of a dyad; a measure of network density i.e. the tendency for all individuals to be connected to all other individuals in the network), with the predictive distribution calculated by Monte Carlo simulations from the fitted model (Gneiting & Raftery, 2004). The cut-off resulting in the lowest CRPS was chosen as representing the 'best' definition of our binary network fitting our model (see Suppl. Mat.).

Results

Data Collected

Of the 160 adult possums collared with proximity-loggers (~50% of the subpopulations), data was retrieved from 49 males and 61 females, comprising 30 787 contacts across April–September 2012. Trapping grids A, B, C and D were represented by data from 35, 27, 26 and 22 collared individuals, respectively; grid A sourced the largest amount of contact data (62%), followed by C, D and B with 15%, 13% and 11% of the total data respectively. Most possums (75%) contacted fewer than 8 different individual possums over the study period (Figure 1).

Network characteristics

Possum social contact networks for the four trapping grids are illustrated in Figure 2, and the network parameters are summarised in Table 2 showing large differences between grids. Relative node degree ($r_{spearman}$ = -0.39, d.f = 3, P = 0.6), edge strength ($r_{spearman}$ = -0.37, d.f = 3, P = 0.62)

and relative betweenness ($r_{spearman}$ = -0.51, d.f = 3, P = 0.48) measures did not correlate with possum density although the small sample size (n=4 locations) limits the power of these comparisons.

Determinants of connectivity

Model exploration indicated that the best ERGM fit to observations was achieved when a network edge was defined as a pair of possums having at least 8 contacts during the study period. The results of the ERGM regression are shown in Table 3. There was a highly significant effect of trapping grid on edge probability, with possums in grids C and D having a higher propensity to be in contact than in the reference grid A (OR 1.17, p=0.00013, OR 1.26, p=0.016 respectively). There was weak (non-significant) evidence that female possums are less likely to be in contact with other females compared to the reference of male-male contacts (OR 0.62, p=0.072), but no evidence that female-male contacts were more or less likely than male-male. As expected, there was strong evidence that possums were highly assortative by their respective trapping grids (OR 26.1, p<0.0001), and having more overlapping home ranges increased the edge probability (although the magnitude of effect was small; OR 1.02, p=0.0018). Finally, possums showed a marked clustering effect beyond that of grid, with the number of edge shared partners being predictive of an edge (OR 2.07, p<0.0001).

Discussion

While the male sex-bias in TB prevalence that is generally observed in wild free-living brushtail possums in New Zealand (Lugton, 1997; Ramsey & Cowan, 2003) has conventionally been assumed to males being more likely to be exposed to other infectious individuals (Montague 2000), our study provides little support for this hypothesis. The inferred mechanism is the larger home ranges of male than female possums (Efford et al., 2000; Yockney et al., 2013; Rouco et al., 2017; Richardson et al., 2017) resulting in them encountering other possums more frequently, with TB transmission among possums being generally reliant on such proximity (see Introduction). However, in the social networks constructed here, adult female possums were generally just as connected with adult male possums as other adult males were, with male-female connection patterns not being significantly different. An important point to clarify here is that the ERGM analysis carried out in the current study did not consider variation in the strength of interactions (i.e. accounting for interaction frequency and duration), but the rate of contacts. Therefore, our results suggest that interaction frequency seems to be unimportant, at least in our study case, to explain sex-bias to the transmission of TB in wild populations, since males interact with other possums apparently at an equal rate to females.

Although having more overlapping home ranges was statistically significant in the model, it was associated with only a small odds ratio and is thus not necessarily ecologically significant. Nevertheless, we needed to account for a measure of home range, such that we can disentangle the tendency for males to meet females from the fact that males move further. This result contrasts with evidence that the observed sex bias is instead driven by TB infected male possums having significantly greater survival rates than TB infected females (Rouco et al. 2016). Possum social network construction is now required for other populations to confirm (or not) the generality of

the connectivity findings presented here, while existing models of TB in possums (e.g. Ramsey & Efford 2010) could be modified to assess whether the observed marked survivorship difference can indeed account for the observed prevalence bias, while the quantified relative connectivity levels among males and females cannot.

Although there was no significant effect of sex on possum connectivity, there were significant differences in possum social network structure among nearby subpopulations within a similar habitat type. Network measures for subpopulations on trapping grids A and C were similar, but had markedly higher measures of node degree and edge strength than those on grids B and D. These patterns were independent of both sampling effort, and the grid differences in possum home range size and population density reported previously (Richardson et al. 2017). However, this is unsurprising given we only studied four subpopulations (and thus had low statistical power to detect between-subpopulation effects) and there was relatively little variation in possum density and sampling effort among grids. The additional possum social network construction for other populations recommended above would thus also provide additional statistical power for these assessments. Also, the level of relatedness among individuals in subpopulations has been shown to influence contact dynamics in other systems (Benton et al. 2016), and thus could be a further factor worthy of investigation as a driver of network structure variation in possums.

While some clarification is forming around the drivers of the observed sex bias in TB prevalence in possums, we still lack good understanding of the wide variation generally observed both temporally within unmanaged populations and spatially among them (Montague 2000, Tompkins et al. 2009). The variation in possum social network structures observed here makes it possible that

such population characteristics play a role through an influence on disease transmission. Should further social networks be constructed for other possum populations, concurrently monitoring TB prevalence would allow this potential link to be explored (with a sufficient population sample size). Likewise, monitoring networks and TB prevalence in populations over time would assess whether similar temporal variation in network structure occurs and is associated with temporal disease dynamics.

Acknowledgements

We would like to thank K. Drew, M. Bridge, J. Smith, S. Hough, N. Fea, S. Brown, D. Clark, B. Karl, C. Thompson, W. Egging, M. Coleman, Mox, C. Niebuhr, A. Friedrich, I. Blasco-Costa, Tb Free NZ, and Cracker for assistance in the field. Funding for this work was provided by the Royal Society of New Zealand Marsden Fund. C. Rouco was also supported by XXII Propio de Investigación of the University of Córdoba and "Programa Operativo de fondos FEDER Andalucía".

References

Arthur, T., Ramsey, D. & Efford, M.G. (2002). Changes in possum behaviour at reduced density– a review. . — In: Landcare Research contract report: LC0102/102. Landcare Research, Palmerston North, New Zealand.

311 Arthur, A., Ramsey, D. & Efford, M.G. (2004). Impact of bovine tuberculosis on a population of
312 brushtail possums (*Trichosurus vulpecula* Kerr) in the Orongorongo Valley, New Zealand.
313 — Wild. Res. 31: 389-395.
314 Barlow, N. (1991). A spatially aggregated disease/host model for bovine Tb in New Zealand
315 possum populations. — J. Appl. Ecol. 28: 777-793.
316 Benton, C.H., Delahay, R.J., Robertson, A., McDonald, R.A., Wilson, A.J., Burke, T.A., Hodg-
317 son, D. (2016). Blood thicker than water: kinship, disease prevalence and group size drive
318 divergent patterns of infection risk in a social mammal. — Proc. R. Soc. B 283: 20160798
319 https://doi.org/10.1098/rspb.2016.0798
320 Buddle, B.M. & Young, L. J. (2000). Immunobiology of mycobacterial infections in marsupials.
321 — Dev. Comp. Immunol. 24: 517-529.
322 Caley, P., Hickling, G.J., Cowan, P.E. & Pfeiffer, D.U. (1999). Effects of sustained control of
323 brushtail possums on levels of *Mycobacterium bovis* infection in cattle and brushtail pos-
324 sum populations from Hohotaka, New Zealand. — N. Z. Vet. J. 47: 133–142.
325 Csardi, G. & Nepusz, T. (2006). The igraph software package for complex network research. —
326 InterJournal 1695: 1-9.
327 Coleman, J. & Caley, P. (2000). Possum as a reservoir of Bovine Tb — In: The brushtail pos-
328 sum: biology, impact and management of an introduced marsupial (Montague, T.L. ed.).
329 Manaaki Whenua Press, Lincoln, p. 92-104.
330 Coleman, J.D, & Cooke, M.M. (2001). *Mycobacterium bovis* infection in wildlife in New Zea-
331 land. — Tuberculosis 81: 191-202.

Corner, L.A.L., Pfeiffer, D.U. & Morris, R.S. (2003). Social-network analysis of *Mycobacterium bovis* transmission among captive brushtail possums (*Trichosurus vulpecula*). — Prev. Vet. Med. 59: 147-167.

Efford, M., Warburton, B. & Spencer, N. (2000). Home-range changes by brushtail possums in response to control. — Wild. Res. 27: 117-127.

Efford, M. & Cowan, P. (2004). Long-term population trend of the brushtail possums (*Trichosurus vulpecula*) in the Orongorongo Valley, New Zealand. — In: The biology of Australian possums and gliders (Goldingay, R.T. & Jackson, S.M. eds.). Chipping Norton, Sidney, p. 471-483.

Fletcher, T. & Selwood, L. (2000). Possum reproduction and development. — In: The brushtail possum: biology, impact and management of an introduced marsupial (Montague, T.L. ed.). Manaaki Whenua Press, Lincoln, p. 62-81.

Gneiting, T. & Raftery, A. E. (2004). Strictly proper scoring rules, prediction, and estimation. Technical Report no. 463. Department of Statistics, University of Washington, Seattle, Washington, USA.

Hunter, D. R., Handcock, M. S., Butts, C. T., Goodreau, S. M., Morris, M. (2008). ergm: A Package to Fit, Simulate, and Diagnose Exponential-Family Models for Networks. Journal of Statistical Software 24: 1–29.

James, A., McLeod, J. C., Rouco, C., Richardson, K. S. & Tompkins, D.M. (2017). Spatial utilization predicts animal social contact networks are not scale-free. — R. Soc. Open Sci. 4: 171209.

Ji, W., White, P.C.L. & Clout, M.N. (2005). Contact rates between possums revealed by proximity data loggers. — J. Appl. Ecol. 42: 595-604.

355 Kenward, R. E. (2001). A Manual for Wildlife Radiotagging. (Academic Press: London.)
356 Livingstone, P.G., Hancox, N., Nugent, G., Mackereth G., Hutchings, S.A. (2015). Development
357 of the New Zealand strategy for local eradication of tuberculosis from wildlife and live-
358 stock. N.Z. Vet. J. 63: 98-107.
359 Lugton, I.W. (1997). The contribution of wild mammals to the epidemiology of tuberculosis
360 (*Mycobacterium bovis*) in New Zealand. — PhD thesis at Massey University, New Zea-
361 land.
362 Matthews, L., Reeve, R., Woolhouse, M., Chase-Topping, M., Mellor, D., Pearce, M., Allison,
363 L., Gunn, G., Low, J. & Reid, S. (2009). Exploiting strain diversity to expose transmission
364 heterogeneities and predict the impact of targeting supershedding. — Epidemics 1:221-
365 229.
366 McCallum, H. (2009). Six degrees of Apodemus separation. — J. Anim. Ecol. 78: 891-893.
367 Montague, T.L., ed (2000). The brushtail possum. Biology, impact and management of an intro-
368 duced marsupial. Manaaki Whenua Press, Lincoln.
369 Morgan, D., Scobie, S. & Arthur, D. (2012). Evaluation of Zoletil and other injectable anaesthet-
370 ics for field sedation of brushtail possums (*Trichosurus vulpecula*). — Anim. Welfare 21:
371 457-462.
372 Morris, R., Pfeiffer, D. & Jackson, R. (1994). The epidemiology of *Mycobacterium bovis* infec-
373 tions. — Vet. Microbiol 40: 153-177.
374 Nugent, G., Sweetapple, P., Coleman, J. & Suisted, P. (2000). Possum feeding patterns: dietary
375 tactics of a reluctant folivore. — In: The brushtail possum: biology, impact and manage-
376 ment of an introduced marsupial (Montague, T.L. ed.). Manaaki Whenua Press, Lincoln, p.
377 10-23.

Nugent, G., Buddle, B. & Knowles, G. (2015). Epidemiology and control of *Mycobacterium bovis* infection in brushtail possums (*Trichosurus vulpecula*), the primary wildlife host of bovine tuberculosis in New Zealand. — N.Z. Vet. J. 1: 28-41.

R Core Team, 2017: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/ [03 June 2017].

Ramsey, D. S. L. & Cowan, D. P. (2003). Mortality rates and movements of brushtail possums with clinical tuberculosis (*Mycobacterium bovis* infection). — N.Z. Vet. J. 51(4): 179-185.

Ramsey, D. S. & Efford, M. G. (2010). Management of bovine tuberculosis in brushtail possums in New Zealand: predictions from a spatially explicit, individual-based model. — J. Appl. Ecol. 47: 911-919.

Ramsey, D. S. L., Coleman, J. D., Coleman, M. C. & Horton, P. (2006). The effect of fertility control on the transmission of bovine tuberculosis in wild brushtail possums. — N. Z. Vet. J. 54: 218-223.

Richardson, K.S., Rouco C., Jewell, C., French, N.P., Buddle, B. M. & Tompkins, D.M. (2017). Investigating brushtail possum (*Trichosurus vulpecula*) home-range size determinants in a New Zealand native forest. — Wild. Res. 44: 316-323.

Robins, G., Pattison, P., Kalish, Y. & Lusher. D. (2007). An introduction to exponential random graph models for social networks. — Social Networks 29:173-191.

Rouco, C., Richardson, K. S., Buddle, B. M., French, N.P. & Tompkins, D. (2016). Sex difference in the survival rate of wild brushtail possums (*Trichosurus vulpecula*) experimentally challenged with bovine tuberculosis. Res. Vet. Sci. 107: 102-105.

399 Rouco, C., Norbury, G.L. & Anderson D.P. (2017). Movements and habitat preferences of pests
400 help to improve population control: the case of common brushtail possums in a New Zea-
401 land dryland ecosystem. — Pest Manage. Sci. 73: 287-294.
402 Silk, M. J. & Fisher, D. N. (2017). Understanding animal social structure: exponential random
403 graph models in animal behaviour research. — Anim. Behav. 132: 137-146.
404 Tompkins, D., Ramsey, D., Cross, M., Aldwell, F., De Lisle, G. & Buddle, B. (2009). Oral vac-
405 cination reduces the incidence of tuberculosis in free-living brushtail possums. — Proc. R.
406 Soc. B 276: 2987-2995.
407 Weber, N., Carter, S.P., Dall, S.R.X., Delahay, R.J., McDonald, J.L., Bearhop, S. & McDonald,
408 R.A. (2013). Badger social networks correlate with tuberculosis infection — Curr. Biol. 23
409 (20) R915-R916.
410 Wickham, H., Francois, R., Henry, L. & Müller, K. (2017). dplyr: A grammar of data manipula-
411 tion. Available at, https://CRAN.R-project.org/package=dplyr.
412 Whyte, B.I., Ross, J.G., & Blackie, H. M. (2014). Differences in brushtail possum home-range
413 characteristics among sites of varying habitat and population density. — Wild. Res. 40:
414 537-544.
415 Yockney, I., Nugent, G., Latham, M., Perry, M., Cross, M. & Byrom, A. (2013). Comparison of
416 ranging behaviour in a multi-species complex of free-ranging hosts of bovine tuberculosis
417 in relation to their use as disease sentinels. — Epidemiol. Infec. 141: 1407-1416.

418 FIGURE CAPTIONS

419

420 **Figure 1** Distribution of the number of possums contacted by collared possums in the Orongo-
421 rongo Valley during the entire study period (data combined across the four trapping grids).

422

423 **Figure 2** Possum social network diagram for each trapping grid, generated by *Igraph* in *R* soft-
424 ware. Numbers located at the nodes denote individual possum IDs with males represented by
425 light grey and females by dark grey nodes respectively. Line thickness is proportional to edge
426 strength. Note that individual placement in diagrams does not represent spatial location.

427

TABLES

Table 1 Definitions of the contact network parameters and the equation notations used in the population-level analysis (Lugton, 1997).

Notations for population level analysis	**Notation Definitions**
Node degree	The number of other possums an individual possum comes into contact with.
Edge strength	The strength of the ties between two nodes or the number of contacts between each pair of possums.
Betweenness	An indicator of a nodes centrality in a given network, the shortest path to all vertices that pass through a given node or how connected a possum is with neighbouring possums.
Equation notations for population level analysis	**Notation Definitions**
I = Node	An individual with a collar.
N = Number of nodes in the network	The number of total collared possums on the individuals trapping grid.
Dc_i = Degree centrality of node i	The measure of the number of contacts node i has.
Bc_i = Betweenness centrality of node i	An estimate of the probability that the shortest path between any pair of nodes of the network passes through node i.
$RDc_i = \frac{Dc_i}{N-1}$; Relative degree centrality of node i	The relative number of total collared possums on the individuals trapping grid used for grid comparison.
$RBc_i = \frac{Bc_i}{(N-1)(N-2)/2}$; Relative betweenness centrality of node i	The relative measure of the number of contacts node i has used for grid comparison.

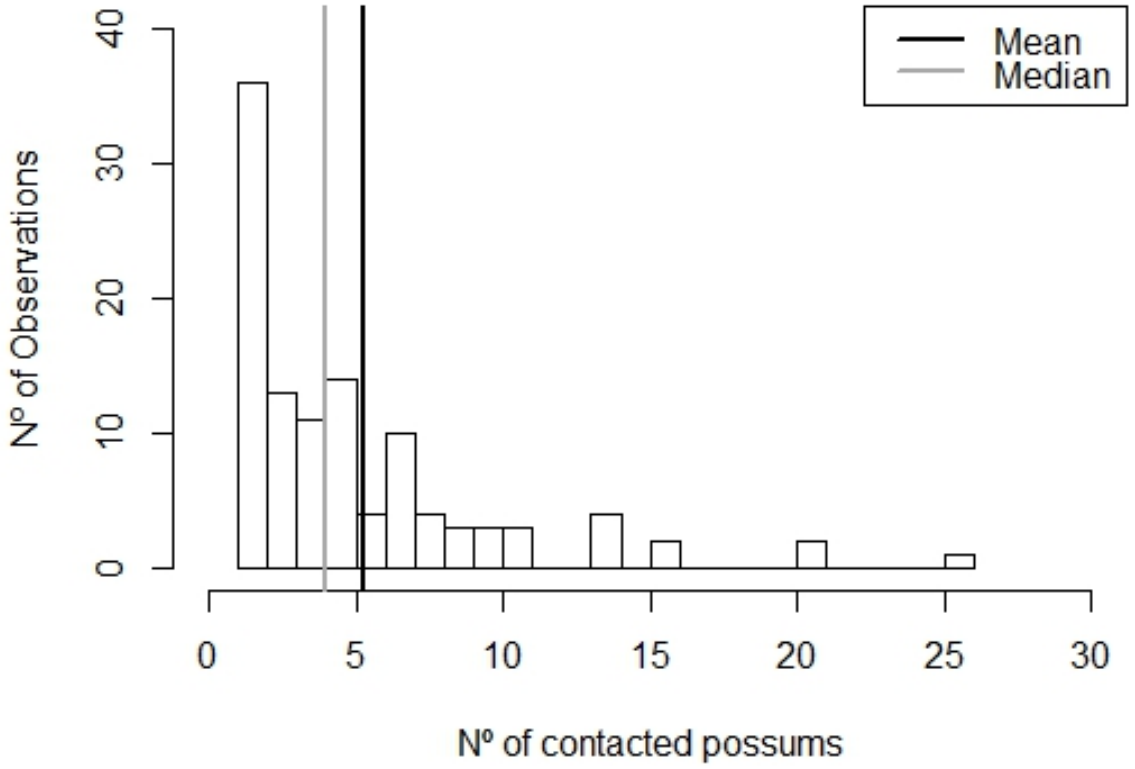
Table 2 Mean (standard error) possum social network characteristics for each trapping grid. Relative values are adjusted for the number of radio-collared individuals in each grid.

Grid	Network parameter estimate (Standard error)				
	Node degree	Relative degree centrality	Edge strength	Betweenness	Relative Betweenness
A	8.5 (0.62)	0.25 (0.02)	309 (43.6)	50.7 (9.5)	0.09(0.02)
B	3.3 (0.48)	0.13 (02)	48.4 (11.2)	6.5 (2.0)	0.02(0.01)
C	15.8 (1.51)	0.63 (0.06)	361 (68.9)	23.6 (6.3)	0.08 (0.02)
D	4.6 (0.63)	0.22 (0.03)	61.6 (16.6)	19.9 (4.4)	0.09 (0.02)

Table 3 Odds ratios for an edge occurring between two possums, given sex, grid assortativity, grid effect, home-range overlap, and the number of geometrically-weighted edge-shared partners (GWESP). The parameter estimate for "Baseline" is interpreted as a probability. Odds ratios for explanatory variables are shown and should be interpreted as the effect on a single edge, conditional on the rest of the network (Hunter et al., 2008).

Explanatory variable		Estimate	*p* value
Baseline edge *probability*		0.00049	$<1 \times 10^{-4}$
Sex combination	Male-Male	1	–
	Male-Female	1.34	0.22
	Female-Female	0.65	0.072
Grid assortativity		26.1	$<1 \times 10^{-4}$
Grid effect	A	1	–
	B	1.19	0.16
	C	1.17	0.00013
	D	1.26	0.015
Number of overlapping home ranges		1.02	0.0018
GWESP		1.75	<0.0001
GWESP decay		1.06	<0.0001

Figure 1


Mean
Median
N° of Observations
0
10
20
30
40
0
5
10
15
20
25
30
Nº of contacted possums

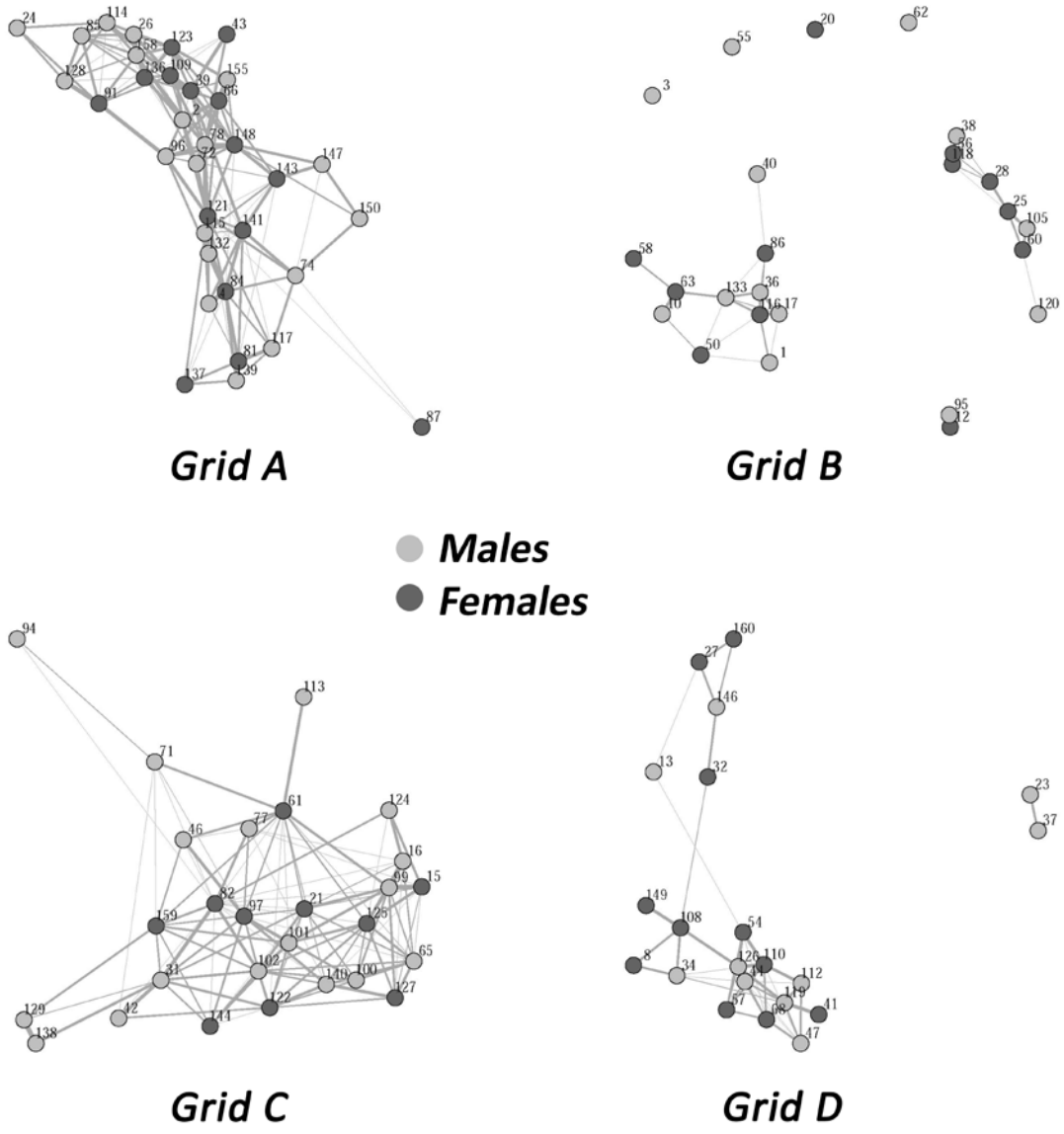



Figure 2