

1 *Title:* Brushtail possum (*Trichosurus vulpecula*) social interactions and their impli-
2 cations for bovine tuberculosis epidemiology

3

4 *Short title:* Possum social networks and TB

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21

22 **Abstract**

23

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

35

36 **Keywords:**

37

38 *Mycobacterium bovis*, Orongorongo Valley, social networks, vertebrate pest

39

40 **Introduction**

41

42 Brushtail possums (*Trichosurus vulpecula*) are medium sized (2 – 3 kg), nocturnal, arboreal mar-
43 supials native to Australia that were introduced to New Zealand in 1858 to establish a fur trade
44 (Montague, 2000). They now occupy most of New Zealand with an estimated population size of
45 30 million (Nugent et al., 2015), and are the main wildlife reservoir for bovine tuberculosis (TB)
46 in the country. Although three other wild mammal species are frequently infected with TB in
47 New Zealand (ferrets, *Mustela furo*; feral deer, *Cervus elaphus*; feral pigs, *Sus scrofa*), they gen-
48 erally serve as ‘spillover’ hosts except for ferrets when they occur in high density (Nugent et al.,
49 2015).

50

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

60

61 The primary route by which possums become infected with *M. bovis* remains unclear but is most
62 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.

108

109 *Study site*

110 The study site was a designated 1200 ha research area in the Orongorongo Valley on the North
111 Island of New Zealand (41°21'S, 174°58'E). The Valley is orientated north to south, runs be-
112 tween steep ridges rising to 670 m above sea level, and contains mixed beech/podocarp forest.

113

114 Data were obtained from four square trapping grids or subpopulations (A, B, C, and D) on the
115 east ridge of the Valley, with grids separated by approximately 650 m. Possum density (\pm SE)
116 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
117 Richardson et al., 2017). Each grid was made up of 100 traps at 40 m spacing covering approxi-
118 mately 13 ha. All trap locations were recorded in the field as Universal Transverse Mercator co-
119 ordinates (UTM) using a Garmin-12 Global Positioning System (GPS) portable receiver. Pos-
120 sums were captured in Grieve wire cage traps (60 cm \times 26 cm \times 28 cm) set on the ground with
121 spring-assisted folding doors triggered by a pendulum bait hook.

122

123 *Data collection*

124 Trapping was carried out at monthly intervals during the study period (April–September 2012),
125 which included the breeding season (April–June; Fletcher & Selwood, 2000). Each session con-
126 sisted of traps being opened and checked for four consecutive nights at each site (with sprung
127 traps reset, and possums recaptured during a trapping session only identified and released). Traps
128 were set and baited each morning with apple sprinkled with powdered sugar and flour lured with
129 anise oil. When first captured, possums were anesthetized by intra-muscular injection of Zoletil
130 100® (Virbac New Zealand Ltd, Auckland, New Zealand) (Morgan et al., 2012), weighed to the

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

134

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

144

145 The data consisted of a separate dataset for each individual on a trapping grid, with each record
146 in a dataset representing a contact between that individual and another individual at the same
147 site. Each record contained the ID of the individual encountered, the time and date at which the
148 encounter occurred, and the length of the encounter. In theory, every encounter should have been
149 recorded twice (i.e. once in the dataset of each interacting individual); however, in practice, only
150 60% of the pairs had fully consistent records for both individuals. Inconsistent records are fre-
151 quently generated by differing alignments of the proximity collars to one another. All contact
152 records from sites B and D were useable. At sites A and C, 34% and 3% of the records respec-
153 tively were discarded because they were either corrupt or because the encounter length was

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

158

159 Within trapping grids there was a structural contact bias meaning that possums located near the
160 centroid of each grid had a greater chance of contacting other collared possums than possums lo-
161 cated on the perimeter of the grids. To control for this bias, the number of possums with overlap-
162 ping home ranges to each contactor over the entire study period was included as an analysis vari-
163 able where relevant. Home ranges were based on the GPS locations of the traps in which each
164 individual was caught. Incremental area analysis (Kenward 2001) was used to determine the ap-
165 propriate number of locations needed to correctly estimate home-range size; home ranges were
166 considered fully revealed when animals were trapped at least 10 times (see Richardson et al.,
167 2017). Individual home ranges were estimated using the 100% minimum convex polygon
168 method (MCP), and the number of overlaps calculated from the geo-located MCPs (implemented
169 in ArcView 3.2, Environmental Systems Research Institute, California, USA).

170

171 *Network characteristics*

172 All analyses were conducted in *R* version 3.4.0. (R Core Team 2017). Collar data was used to
173 characterize the subpopulation network structure separately for possums on each of the four trap-
174 ping grids. Network parameters included node degree, edge strength and betweenness (see Table
175 1 for definitions and references for these measures). To standardize data for cross-grid compari-
176 sons, relative values for node degree and betweenness were estimated (see Table 1 for notation

177 definitions and equations); i.e. relative degree centrality (RDC_i) and relative betweenness central-
178 ity for undirected networks (RBC_i) (Lugton, 1997). Edge strength does not need to be corrected
179 for the size of the network, being the number of contacts between each pair of possums. Pack-
180 ages *Dplyr* (Wickman et al., 2017) and *Igraph* (Csardi & Nepusz, 2006) were used to set up a
181 working database and to construct network graphs/webs for viewing the distribution of contacts
182 between individuals. Spearman rank correlations were used to compare social network parame-
183 ters and possums density per grid using the *cor()* function.

184

185 *Determinants of connectivity*

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

198

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

208

209 **Results**

210

211 *Data Collected*

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

218

219 *Network characteristics*

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

223 and relative betweenness ($r_{\text{spearman}} = -0.51$, d.f = 3, $P = 0.48$) measures did not correlate with pos-
224 sum density although the small sample size ($n=4$ locations) limits the power of these compari-
225 sons.

226

227 *Determinants of connectivity*

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

241

242 **Discussion**

243

244 While the male sex-bias in TB prevalence that is generally observed in wild free-living brushtail
245 possums in New Zealand (Lugton, 1997; Ramsey & Cowan, 2003) has conventionally been as-
246 sumed to males being more likely to be exposed to other infectious individuals (Montague 2000),
247 our study provides little support for this hypothesis. The inferred mechanism is the larger home
248 ranges of male than female possums (Efford et al., 2000; Yockney et al., 2013; Rouco et al.,
249 2017; Richardson et al., 2017) resulting in them encountering other possums more frequently,
250 with TB transmission among possums being generally reliant on such proximity (see Introduc-
251 tion). However, in the social networks constructed here, adult female possums were generally
252 just as connected with adult male possums as other adult males were, with male-female connec-
253 tion patterns not being significantly different. An important point to clarify here is that the
254 ERGM analysis carried out in the current study did not consider variation in the strength of inter-
255 actions (i.e. accounting for interaction frequency and duration), but the rate of contacts. There-
256 fore, our results suggest that interaction frequency seems to be unimportant, at least in our study
257 case, to explain sex-bias to the transmission of TB in wild populations, since males interact with
258 other possums apparently at an equal rate to females.

259

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

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

271

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

285

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

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

296

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306 **References**

307

308 Arthur, T., Ramsey, D. & Efford, M.G. (2002). Changes in possum behaviour at reduced den-
309 sity– a review. . — In: Landcare Research contract report: LC0102/102. Landcare Re-
310 search, 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.

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

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

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

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

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

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

350 James, A., McLeod, J. C., Rouco, C., Richardson, K. S. & Tompkins, D.M. (2017). Spatial utili-
351 zation predicts animal social contact networks are not scale-free. — *R. Soc. Open Sci.* 4:
352 171209.

353 Ji, W., White, P.C.L. & Clout, M.N. (2005). Contact rates between possums revealed by proxim-
354 ity 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.

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

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

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

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

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

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

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

396 Rouco, C., Richardson, K. S., Buddle, B. M., French, N.P. & Tompkins, D. (2016). Sex differ-
397 ence in the survival rate of wild brushtail possums (*Trichosurus vulpecula*) experimen-
398 tally 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.
D _{c_i} = Degree centrality of node i	The measure of the number of contacts node i has.
B _{c_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.
$RD_{c_i} = \frac{D_{c_i}}{N-1}$; Relative degree centrality of node i	The relative number of total collared possums on the individuals trapping grid used for grid comparison.
$RB_{c_i} = \frac{B_{c_i}}{(N-1)(N-2)/2}$; 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 (0.02)	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)

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

Explanatory variable		Estimate	<i>p</i> value
Baseline edge <i>probability</i>		0.00049	<1 x 10 ⁻⁴
Sex combination	Male-Male	1	–
	Male-Female	1.34	0.22
	Female-Female	0.65	0.072
Grid assortativity		26.1	<1 x 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

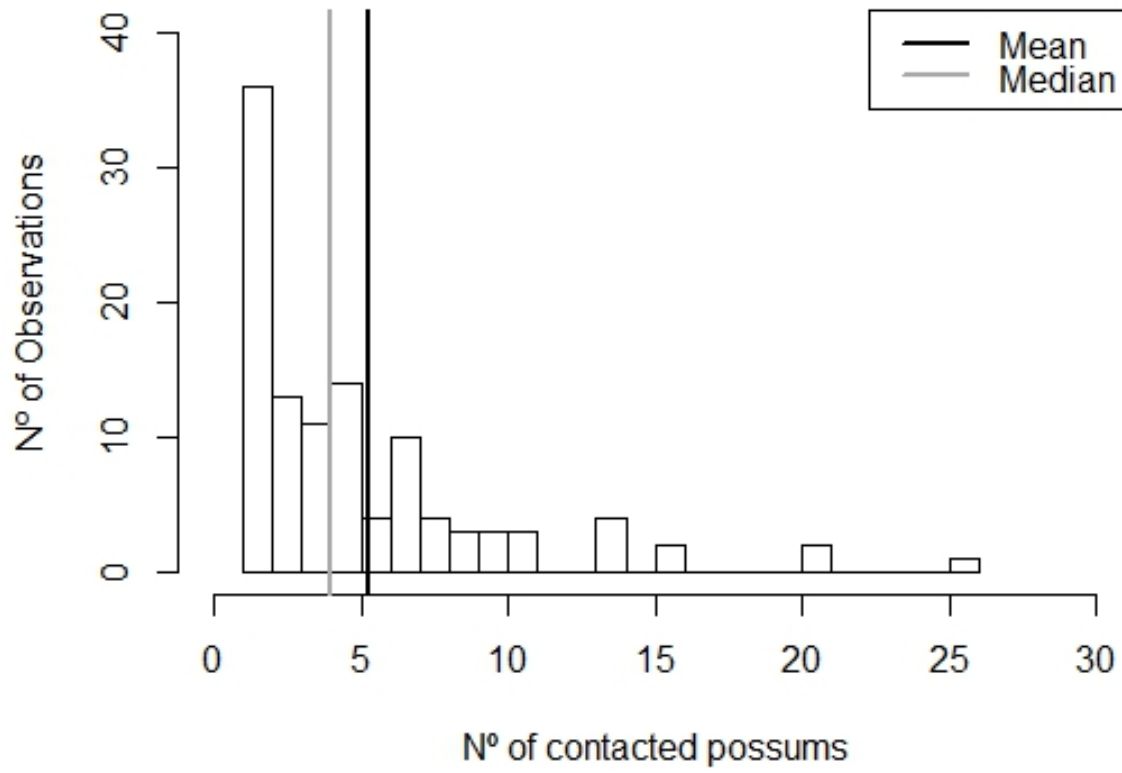
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9 **Figure 1**

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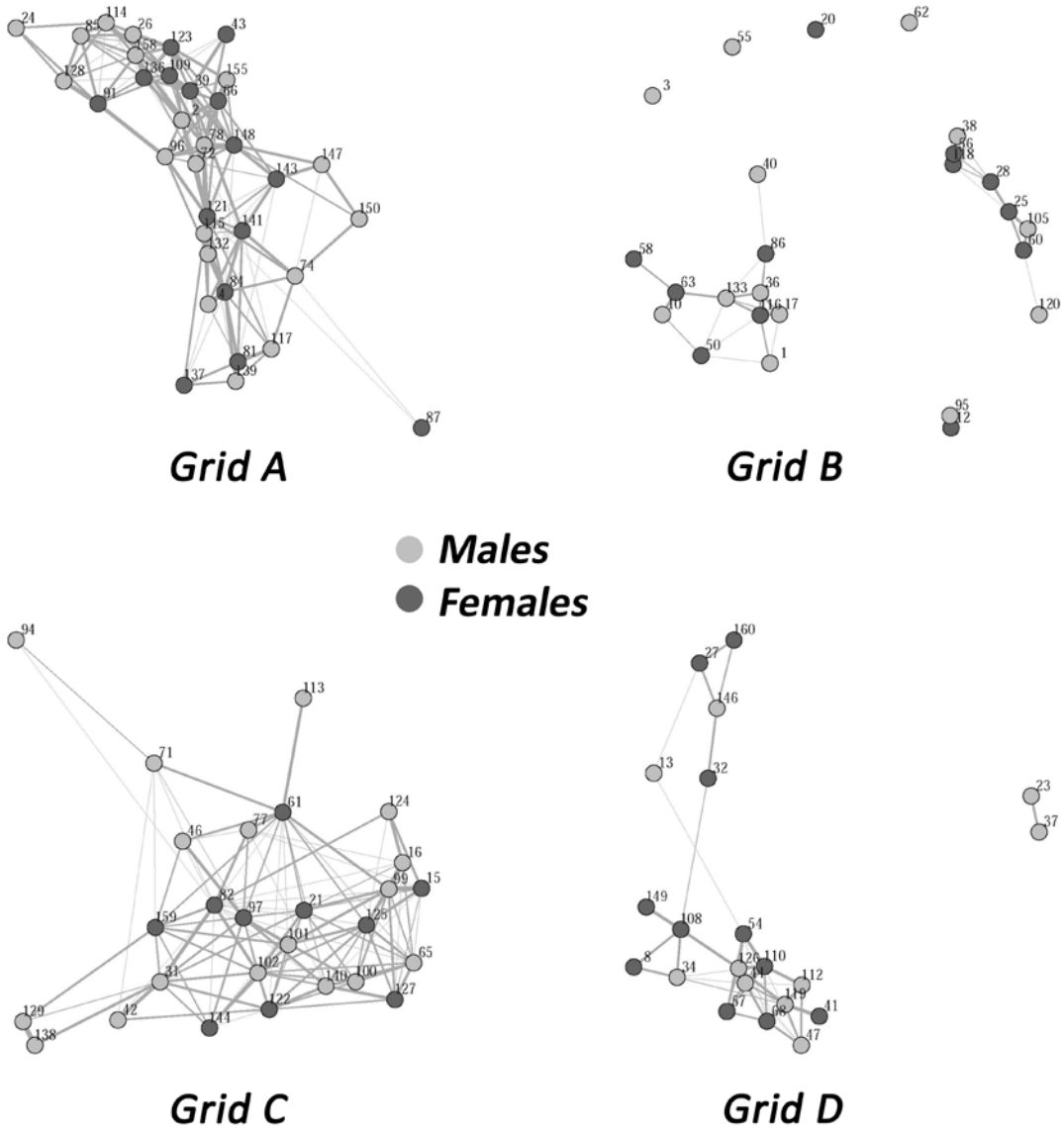


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13 **Figure 2**

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