

25 **Key-words:** Contact network, DFTD, disease transmission, infectious disease,
26 network analysis, Tasmanian devil, transmission event

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29 **LAY SUMMARY**

30 Pinpointing potential incidences of disease transfer is extremely difficult. In
31 Tasmanian devils a transmissible form of cancer transfers between devils when they
32 bite one another, in competitive and mating interactions. Therefore, behaviours
33 resulting in bite wounds present clear transmission pathways. By examining contact
34 and bite wound patterns in a devil population, we highlight males who spend long
35 periods in mating consorts with females as potentially important drivers of disease
36 spread.

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48 **INTRODUCTION**

49 Emerging infectious diseases (EIDs) are a major threat to biodiversity globally (De
50 Castro and Bolker 2005; Smith et al. 2006). EIDs frequently impact populations that
51 are already declining, thereby exacerbating the effects of habitat degradation,
52 pollution, human-wildlife conflict or climate change (Blaustein et al. 2011; Heard et
53 al. 2013). An increasing number of EIDs are recognized to cause severe population
54 declines, including two species of chytrid fungus in amphibians (Stuart et al. 2004;
55 Martel et al. 2014) and white-nose syndrome in bats (Blehert et al. 2009). However,
56 the transmission dynamics by which infectious diseases spread through natural
57 populations are not well understood. Evaluating how contact patterns affect the
58 transmission dynamics of infectious diseases within and among populations is an
59 urgent priority for management of infectious disease and endangered species
60 conservation.

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62 Patterns of interaction among individuals have major consequences for disease
63 dynamics of directly transmitted pathogens, including transmission, and the rate and
64 spatial scale of spread (Kappeler et al. 2015; Arthur et al. 2017). In highly social
65 species, such as group-living mongooses (Drewe 2010) and most primates (MacIntosh
66 et al. 2012; Carne et al. 2014), individuals associate closely within social groups and
67 groups interact regularly, often in territorial conflicts or out-breeding events (Madden
68 et al. 2009; Weber et al. 2013). Regular interaction between group members facilitates
69 rapid disease spread within groups, while inter-group contacts allow disease spread
70 among groups and between populations (Craft et al. 2011). Patterns of disease
71 transmission are more varied in solitary species, where interactions between
72 individuals are less frequent, and the extent of the effect can be influenced by

73 population size and density (Caillaud et al. 2006; Langwig et al. 2012). In solitary
74 species, spread of pathogens (particularly those requiring direct contact for
75 transmission) generally occurs during specific events, such as mating (Ganguly et al.
76 2016) or competition over resources (Wright and Gompper 2005). In these cases, the
77 familiarity of individuals may influence the likelihood of a successful transmission
78 event (Vander Wal et al. 2012; VanderWaal et al. 2016; Hasenjager and Dugatkin
79 2017). For example, familiar individuals may have an established dominance
80 hierarchy that seldom requires physical interaction. Consequently, unfamiliar
81 individuals may be more likely to have physical confrontations (Brunton et al. 2008;
82 Robinson et al. 2015), thereby heightening the chance of pathogen transfer. Thus,
83 identifying the circumstances under which transmission is likely to occur is important
84 for understanding disease dynamics.

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86 Social network analysis is increasingly used as a tool for understanding process flows
87 through biological systems (Krause et al. 2007; Aplin et al. 2015; Craft 2015; Silk et
88 al. 2017a; White et al. 2017) as it facilitates analysis of how contact patterns at the
89 individual level, and network structures at the population level, influence transmission
90 dynamics (Rushmore et al. 2013; Rimbach et al. 2015). Studies of information
91 transfer (e.g. discovery of resource patches, novel foraging methods) have revealed
92 patterns relating to networks both within and between species, and how these affect
93 information flow (Aplin et al. 2012; Farine et al. 2012; Aplin et al. 2015; Firth et al.
94 2016). Emerging patterns that link an individual's centrality (the various properties of
95 its position in a community; Borgatti 2005) within a network to its influence on
96 transmission dynamics have been uncovered in multiple processes, particularly
97 information flow (Aplin et al. 2012; Allen et al. 2013), parasite load (Godfrey et al.

98 2010; VanderWaal et al. 2014) and disease spread (Drewe 2010; Weber et al. 2013;
99 Silk et al. 2018). Key metrics relating to transmission include *degree* (representing
100 either the total number of interactions individuals have, or the total number of other
101 individuals they interact with), *betweenness* (number of shortest paths between nodes
102 in the network that flow through an individual) and *clustering coefficient* (probability
103 that an individual's neighbours are also well connected). For example, individuals that
104 regularly engage in behaviors involving direct interactions (e.g. mate prospecting,
105 grooming) will have high scores for degree metrics, while individuals that act as
106 bridges between disparate groups are easily identifiable by high betweenness (Weber
107 et al. 2013). Both tendencies inflate risk of pathogen transmission (Drewe 2010;
108 MacIntosh et al. 2012), and can play key roles in transmission dynamics. In extreme
109 cases, such individuals can be superspreaders (Lloyd-Smith et al. 2005) responsible
110 for the majority of infections in a population, and thus those that are particularly
111 important to identify as potential targets for intervention.

112

113 The Tasmanian devil and its transmissible cancer, devil facial tumour disease
114 (DFTD), provide an excellent study system to quantitatively assess infection risk
115 using contact networks. Devils are under threat from DFTD, which is transmitted
116 when live tumour cells, the pathogenic agent (Pearse and Swift 2006), are transferred
117 from infected to susceptible individuals when they bite one another (Hamede et al.
118 2013). Individuals that develop DFTD almost invariably die within 6-12 months of
119 clinical symptoms appearing (Loh et al. 2006; Hamede et al. 2012; Wells et al. 2017).
120 The key to understanding the transmission dynamics of DFTD and modelling its
121 spread is establishing the patterns of contact that result in bite wounds (Hamede et al.
122 2013). In devils, the most common type of contacts, such as those between individuals

123 with overlapping home ranges (Guiler 1970) and at regular aggregations around food
124 sources (Pemberton and Renouf 1993), are most likely to be benign with little or no
125 injurious biting. Using proximity loggers (radio-collars capable of logging when
126 individuals come in close proximity) to investigate contact networks in wild devils,
127 Hamede et al. (2009) found that all devils in a population were connected in a single
128 network and that contact frequencies were higher during the mating season, but the
129 relationship between contact rates and the likelihood of being bitten was not assessed.

130

131 In this study, we examine contact patterns and bite wound accrual simultaneously in a
132 DFTD-free wild population of Tasmanian devils using proximity loggers coupled
133 with regular captures. Through multi-model inference, we investigate contact patterns
134 among individuals, their position in the social network and propensity to accumulate
135 bite wounds. We explore the effect of sex and familiarity of contact partners on the
136 likelihood of receiving bite wounds, which constitute potentially disease-transferring
137 contacts. Understanding the identity and interaction patterns of those individuals
138 likely to be involved in disease transmission events could guide management of
139 DFTD spread in populations not yet affected by the disease. These analyses afford a
140 new perspective on the potential of different types and contexts of social contacts to
141 transmit disease in a wild population.

142

143 **MATERIALS AND METHODS**

144 **Proximity loggers**

145 We used proximity data loggers fitted to adjustable collars (Sirtrack E2, Havelock
146 North, New Zealand) to record interactions between devils. Each logger emits a
147 unique UHF pulse so that when two, or more, loggers are within a pre-determined

148 distance of one another (calibrated via UHF detection range) the time, date, encounter
149 length and unique logger number(s) are recorded and stored on the devices internal
150 memory. Collars also incorporated a VHF component, on a separate circuit and
151 battery, so the animals could be located. The entire collar assembly weighed 120g –
152 less than 2.5% of the body weight of the smallest individual collared.

153

154 To ensure that only contacts with the potential to lead to DFTD transmission were
155 recorded, loggers were calibrated to detect and interrogate one another at a distance of
156 30 cm or less. This represents the physical distance at which devils could conceivably
157 bite one another, and hence transfer disease (see Hamede et al. 2009 and Hamede et
158 al. 2013 for further rationale). Loggers were programmed to have a separation time of
159 10 seconds, meaning that a single encounter was recorded by each device until they
160 had failed to detect one another for a period of 10 seconds or more. Prior to
161 deployment in the wild, detection distances for each individual collar were calibrated
162 and then tested in a laboratory setting, as well as with captive devils at Bonorong
163 Wildlife Sanctuary (see Supplementary Materials 1 for details of each collars
164 performance).

165

166 Upon collar retrieval, data from each individual were filtered to ensure that there was
167 symmetry between collar data for each dyad. For all interactions greater than one
168 second that were logged by both collars in a dyad we took the time between when the
169 first collar commenced logging and when the last collar terminated logging as the
170 interaction duration. Contacts of one second duration were eliminated from the
171 dataset, as these represent “phantom contacts” – the result of collars being just outside

172 detection range and incorrectly decoding faint signals as contact events (Prange et al.
173 2006).

174

175 As all individuals were fitted with collars for slightly different time periods (all
176 animals were collared on different days, while 3 individuals died as a result of vehicle
177 collision during the study period) all terms relating to interactions were calculated as
178 rates as opposed to absolute numbers. For each dyad between animals their interaction
179 rate was calculated as the total number of interactions within the dyad divided by the
180 number of days that both individuals were collared concurrently. This resulted in an
181 interaction rate for each pairing of individuals, which were then summed to calculate
182 each individual's total interaction rates with different classes of interaction partners;
183 the rate for each dyad was used as an edge between interaction partners during
184 network calculations. This standardisation of interaction rates accounts for slight
185 differences in sampling effort between individuals (Farine and Whitehead 2015;
186 Blaszczyk 2017)

187

188 **Study site and data collection**

189 The study was conducted in the northern section of the Arthur Pieman Conservation
190 Reserve, north of the Arthur River, in north-western Tasmania (-40.999 E, 144.649
191 S). The population was not affected by DFTD throughout the study period. Habitat in
192 this area predominantly consists of coastal scrub and eucalypt forest dominated by
193 *Eucalyptus obliqua* and *E. nitida*.

194

195 Tasmanian devils were caught for collaring by setting 35 traps over a 25 km² area for
196 a period of one month. Traps were custom built of 300 mm polypipe and baited with a

197 variety of meats. The population of devils used for the study had been surveyed
198 regularly for two years prior; therefore we had previous knowledge of which
199 individuals were resident and which were vagrants (see Supplementary Materials 2 for
200 details of the background population). All sexually mature devils (two years of age
201 and older) trapped in the study area with a trap history that indicated they were
202 residents of the core area were fitted with collars between January and March 2015
203 (12 females, 10 males). Geographical barriers to the south (the deep and 20 - 100m
204 wide Arthur River), east (wide tracts of open paddock) and west (the Indian Ocean)
205 limit movement of new adult individuals into the population. Proximity collars were
206 activated and collecting contact data on devils from January until the end of June
207 2015. This timespan encompasses both mating (February to April) and non-mating
208 periods (May to June), so differences in contact rates between reproduction-relevant
209 seasons could be assessed. The timing of the mating season was determined by
210 backdating birth date and pregnancy based on the developmental stage and size of
211 pouch young (see Hesterman et al. 2008 and Hamede et al. 2009 for further details).
212
213 Collared devils were re-trapped monthly throughout the study period to document
214 new wounds as they occurred, as well as to assess collar fit. Only wounds that
215 penetrated the dermis were recorded, as these are the injuries that have the potential to
216 result in DFTD transfer. The period between captures of each individual was
217 generally a month or less, meaning that new wounds were unlikely to have healed
218 between captures (penetrating wounds in Tasmanian devils take three to eight weeks
219 to heal to a point at which they are undetectable, depending on their severity).
220 Positions of wounds on the animal were recorded and photographed on each capture
221 so that new wounds could be identified on future captures (see Supplementary

222 Materials 3 for examples). Since agonistic interactions with other predators (spotted-
223 tailed quolls, *Dasyurus maculatus*, and feral cats, *Felis catus*) are extremely rare
224 (Jones 1995), all wounds recorded are likely to have come from conspecifics.

225

226 **Network construction and statistical analyses**

227 Contact networks were constructed in the *igraph* package in R v3.2.5 (R Core Team
228 2014) using the filtered contact rate in each dyad. Networks were separated into
229 mating (15th February - 15th April) and non-mating (Jan – 15th February and 15th April
230 – 31st June) seasons. Individuals were represented as nodes linked by observed contact
231 rates. The size of nodes represented the number of wounds individuals received over
232 the course of each season, while lines between nodes (edges) were weighted by the
233 rate of contacts. Network metrics and properties (detailed later) were also calculated
234 using *igraph*.

235

236 We investigated the relationship between individual interactions and the number of
237 wounds that devils accumulated over the course of the study for all 22 devils in the
238 adult population. We used generalized linear mixed models (GLMMs) with Poisson
239 error to assess the effects on the number of bite wounds of two categorical variables
240 (sex and season) and four continuous variables describing modes of interactions: 1)
241 rate of interactions of less than one minute, 2) rate of interactions of more than one
242 minute, 3) proportion of hours spent in extended pairings with opposite sex and 4)
243 proportion of hours spent in extended pairings with the same sex). Interactions
244 totalling less than one minute represent brief contacts, where individuals come into
245 close proximity for a short period, while interactions totalling more than one minute
246 represent prolonged interactions. The hours spent in extended pairings with the

247 opposite sex represent two devils sharing a den in close proximity. Regular physical
248 confrontation can occur during these periods, which last from 1 – 13 days as males
249 attempt to restrain females from departing during their oestrous. Hours spent in
250 extended pairings with the same sex represent intra-sex den sharing – it is likely that
251 these events represent devils tolerating each other’s presence, although physical
252 aggression could occur during such encounters. To account for small sample size ($n =$
253 22 individuals over two seasons), we included no more than three independent
254 variables per model and no more than five models in each analysis. Based on *a priori*
255 knowledge (Hamede et al. 2013), and clear patterns in the results, that a) devils
256 acquire more wounds in the mating season, and b) males acquire more wounds than
257 females (see Fig. 2), the categorical variables accounting for sex and season (and an
258 interaction term between them) were retained in the majority of models. Each model
259 contained one random factor, individual, to account for the models including data
260 separated into seasons (mating and non-mating) for each individual. The null model
261 contained only the random factor.

262

263 We developed model hypotheses related to the factors potentially influencing biting
264 contacts (and therefore potential transmission of DFTD) in devils, to derive the best
265 prediction of the number of bite wounds an individual received over the course of the
266 mating and non-mating seasons. We used a multi-model inference approach
267 (Burnham and Anderson 2002), ranking models using Akaike’s Information Criterion
268 corrected for small sample size (AICc). All models were run using the *lme4* and
269 *AICcmodavg* packages in R v3.2.5 (R Core Team 2014). See Supplementary
270 Materials 4 for a list of all models run.

271

272 We then investigated the relationship between the identity of an individual's
273 interaction partners and the number of bite wounds it received in a further set of
274 GLMMs (using the same multi-model inference approach and packages as detailed
275 above). For this analysis, we measured the effect of the regularity with which an
276 individual interacted with their dyadic partners, as well as the sex of those dyadic
277 partners, on the number of bite wounds they received. To quantify the regularity of
278 contact with interaction partners, each dyad was ranked as "*weak*" (rate of 0 to 0.1
279 interactions per day), "*intermediate*" (rate of 0.1 to 0.5 interactions per day) or
280 "*strong*" (rate of > 0.5 interactions per day) ties. These represent the regularity of
281 contact between pairs of individuals and may affect likelihood of involvement in a
282 physical interaction with one another. Analyses were run using both more and less
283 generous cut-off frequencies for "*weak*" (rate of 0.05 through 0.4 per day),
284 "*intermediate*" (rate of 0.05 through 1 per day) and "*strong*" (0.5 through 2 or more
285 per day) dyads, but patterns remained identical at the varying thresholds. The dyadic
286 ranking thresholds used in the final models divide the observed data into three
287 approximately equal groups. We assessed the effects of two categorical variables (sex
288 and season) and five continuous variables (rate of interactions in "*weak*" dyads, rate
289 of interactions in "*intermediate*" dyads, rate of interactions in "*strong*" dyads, rate of
290 interactions with males and rate of interactions with females) on the number of bite
291 wounds acquired by individuals. The same random factor (individual) as in the
292 previous set of models was included in all models, including the null model.
293
294 Finally, to establish the influence of an individual's position within a network
295 (network metrics) on its propensity to pick up bite wounds, we applied network
296 autocorrelation models (NAMs; R package *tnam*) to the contact networks for mating

297 season and non-mating season respectively. In each model, sex and age were fitted as
298 fixed effects, while terms were fitted for social network metrics which are likely to
299 have an influence on disease transmission, specifically: 1) weighted degree (the
300 proportion of individuals in a population that an individual associates with); 2)
301 betweenness centrality (the number of shortest paths that flow through a node); 3)
302 closeness centrality (metric based on the sum of shortest paths that run through a
303 node); and, 4) clustering coefficient (measure of how many of a node's connections
304 are also connected). None of these network metrics were significantly correlated with
305 one another. Each network term was centred, while the inherent non-independence of
306 connected individuals in the network was accounted for using a *weightlag* term in the
307 model. All network centrality measures examined provide indications of how
308 influential an individual will be in the event of disease spreading through a
309 population. If these metrics relate to the number of potentially disease-causing bite
310 wounds an individual receives, they provide a proxy for the role of that individual in
311 DFTD transmission in the case of an outbreak. We also tested for differences in bite
312 wounds and social network metrics between sexes and seasons using node-permuted
313 t-tests, comparing to 10,000 randomized t-statistics to account for non-independence
314 (Croft et al. 2011).

315

316 **RESULTS**

317 **Influence of individual interactions**

318 The most important predictor of the number of bite wounds received was the
319 proportion of hours an individual spent in extended inter-sex contacts. This effect was
320 sex specific. Under the single best fitting model males accrued one additional bite
321 wound for every 42.59 hours spent in extended inter-sex contacts in the breeding

322 season; no pattern was apparent for females. This model, which accounted for 81% of
323 AICc weight, included this factor alongside the categorical variables sex and season
324 (see Table 1a). A second model (incorporating rate of contacts of less than one
325 minute, sex and season) was separated from the first model by just over three units of
326 AICc ($\Delta\text{AICc} = 3.08$) and accounted for 17% of AICc weight (see Table 1a). Other
327 models had much greater steps in AICc.

328

329 **Influence of interaction partners**

330 The more time male devils spent in strong dyads, the more likely they were to
331 accumulate bite wounds. The best supported model in the analysis of influence of
332 dyad partners contained the factors strong ties (interaction rate of > 0.5 per day), sex
333 and season, and accounted for 93% of AICc weight (see Table 1b). A second model,
334 explaining 7% of AICc weight ($\Delta\text{AICc} = 5.05$), contained the number of contacts with
335 female interaction partners. The models containing weak and intermediate ties
336 received no support (see Table 1b).

337

338 **Influence of network position**

339 None of the network metrics examined provided a strong predictor of the number of
340 bite wounds an individual received. The only factor found to influence number of bite
341 wounds accrued was the sex of the individual, again with males more likely to obtain
342 bite wounds in the mating season (see Table 2). Similarly, none of the network
343 metrics examined proved to be a strong predictor of the number of bite wounds
344 accrued in the non-mating season (see Table 2).

345

346 Contact networks were comprised of one large component (i.e. all individuals were
347 connected, either directly or indirectly) during both the mating and non-mating
348 seasons (Fig. 1). The number of wounds received by devils differed significantly
349 between seasons ($P = 0.005$; paired t-test), and between sexes during the mating
350 season ($P = 0.026$), with a higher number of wounds being received by males,
351 particularly during the mating season (see Fig. 2). The only network metrics which
352 differed between seasons were closeness centrality, which was significantly higher
353 during the mating season ($P = < 0.001$), and clustering coefficient, which was
354 significantly higher during the non-mating season, particularly in females ($P = 0.019$;
355 see Table 3).

356

357 **DISCUSSION**

358 Identification of potential disease transmission events, and their occurrence within
359 contact networks, is critical for understanding the dynamics of disease spread (Craft
360 2015; Chen and Lanzas 2016; Manlove et al. 2017). Here, we conducted a contact
361 network study in Tasmanian devils while simultaneously examining potential disease
362 transmission events. Divergences between sexes and seasons were identified which
363 are likely to have significant consequences for the spread of disease in Tasmanian
364 devils. Males acquired more dermis-penetrating bite wounds with the potential to
365 facilitate DFTD transmission than females, and these occurred mostly during the
366 mating season. Acquisition of bite wounds in males was highly correlated with time
367 spent in extended contacts with females, particularly those with whom they interacted
368 regularly. These results contribute to our understanding of disease susceptibility and
369 how it relates to variations in contact patterns between individuals (Altizer et al. 2006;
370 Blyton et al. 2014; Han et al. 2015).

371

372 Our use of proximity loggers indicated that the mating season wounds received by
373 males were associated with extended associations with females (lasting 1-13 days),
374 shedding doubt on a previously held perception that the large number of injuries in
375 males during the mating season result from male—male combats aimed at accessing
376 females (Hamede et al. 2008). Instead, male—male interactions were rare during the
377 mating season and their rate of occurrence was not associated with frequency of
378 injuries. This result corroborates the findings of Hamede et al. (2009) that devil
379 mixing patterns during the mating season were almost entirely inter-sexual. Our
380 additional examination of the bite wounds devils accrued whilst involved in
381 interactions with other devils has allowed insights into the potential of these
382 associations to result in disease transfer. Mate guarding behavior is seen in devils
383 (Jones, *unpublished*) and a variety of other species (Taggart et al. 2003), and involves
384 males attempting to exclude other males from access to a female in oestrous to
385 increase the guarder's chance of paternity. Guarding behavior can involve high levels
386 of aggression towards competing males (Girard-Buttoz et al. 2014; Baxter et al.
387 2015), and can also be associated with aggression between the male and the female
388 being guarded (Elias et al. 2014), including in devils (Jones, *unpublished*). Our results
389 suggest that males are being wounded while guarding females in oestrus, and the
390 longer they spend engaged in this type of behavior, the more wounds they receive.
391 This highlights the potential for mating interactions to enhance disease transmission,
392 and is consistent with recent findings that Tasmanian devils with a high reproductive
393 output are more likely to contract DFTD during their lifetime (Wells et al. 2017). Use
394 of proximity collars has provided new insights into the mating behavior of devils, a

395 cryptic, nocturnal species that is difficult to observe directly in the wild, particularly
396 mating interactions that usually occur in underground burrows.

397

398 Networks of contact rates between devils were comparable with a previous study of
399 contact networks within the species (Hamede et al. 2009). In both studies, networks
400 for the mating and non-mating seasons were comprised of one large component, male-
401 male interactions were relatively rare and extended male-female interactions made up
402 the bulk of contacts during the mating season. While values for degree and
403 betweenness were higher in the 2009 study (see Hamede et al. 2009 and Table 3),
404 network density was comparable, indicating divergences can likely be attributed to the
405 higher number of nodes in the earlier networks. This suggests that large scale patterns
406 observed in devil networks, particularly pertaining to the mating interactions that are
407 potentially critical to disease transfer, are relatively consistent between populations.

408

409 Given that a high proportion of potentially disease-transmitting bite wounds occurred
410 during the mating season, particularly during mate-guarding, how does this compare
411 to observations of patterns of the transmission of DFTD? Unfortunately, the disease
412 does not have a consistent latent period, with the limited information available on
413 time from transmission event to development of clinical signs ranging from 3 weeks
414 (in experimental trials) to 11 months in the wild (asymptomatic individual developing
415 tumours after being brought into captivity). This variability in latent period obscures
416 any potential seasonality in the transmission of the disease (Hamede et al. 2009;
417 McCallum et al. 2009). Additionally, there is no evidence from extensive mark-
418 recapture data that DFTD prevalence differs between the sexes (Hawkins et al. 2006;
419 McCallum et al. 2009; Hamede et al. 2012; 2015). This lack of sex bias in disease

420 prevalence seems to contradict our results, which indicate that males are more likely
421 to obtain potentially disease-transmitting wounds. However, most injuries to males
422 were associated with their interaction rate with females, as opposed to their rate of
423 interaction with males, which supports a lack of sex bias in disease prevalence
424 (further explored in the following paragraph). Outside of the mating season, the rate
425 of biting injuries and most network metrics are more even between the sexes and the
426 rate of injurious biting is lower than that during the mating season. However,
427 cumulatively over the course of the year the number of injuries is still substantial and
428 likely to have an influence on DFTD transmission. Notably, both sexes display
429 heightened levels of clustering (meaning they are well connected to other well-
430 connected individuals within the network; see Fig. 1 and Table 3) outside the mating
431 season, which may increase their probability of coming into contact with a diseased
432 individual (even though their total number of potentially disease-causing interactions
433 is lower). This additional potential for exposure to diseased individuals outside the
434 mating season would result in DFTD continuing to spread through the population
435 even during periods when the seemingly critical mating interactions are not occurring.
436 Further studies of the contact patterns of devils in DFTD-affected populations are
437 required to identify additional vulnerable periods throughout the year and to fully
438 explain the lack of sex bias observed in DFTD prevalence.

439

440 In terms of relating our findings to real time transmission of DFTD in the wild, there
441 is uncertainty concerning the dominant direction of disease transfer. Transmission
442 could occur by devils biting the tumour of another animal, or by having live tumour
443 cells inoculated when they are bitten. Empirical data support the former possibility, as
444 devils that have fewer bite wounds are more likely to acquire the disease (Hamede et

445 al. 2013). This led to the hypothesis that more dominant animals were biting
446 subordinate animals, possibly into their tumours, and becoming infected (Hamede et
447 al. 2013), which appears consistent with model results suggesting individuals with
448 higher reproductive success were more likely to acquire DFTD (Wells et al. 2017).
449 The results presented here, and observations of devil mating behavior in captivity
450 (Jones, *unpublished*), suggest that both sexes bite each other during mating
451 interactions, but females cause a higher number of injuries (to the males) during the
452 mating season, when there is also an annual spike in biting injuries (Hamede et al.
453 2013). Insights into cryptic devil behavior are beginning to overturn our assumptions
454 about male dominance in aggressive encounters and suggests that males could be
455 critical to transmission dynamics during the mating season, as they are involved in
456 high numbers of interactions as either the potential vector or recipient of DFTD cells.
457 However, it remains unclear what proportion of transmission incidences result from
458 biting or from being bitten. A combination of both forms of transmission would
459 reconcile the lack of sex bias in DFTD prevalence with our results. Further
460 understanding of the directionality of disease transfer is required before we can fully
461 ascertain how DFTD travels through devil populations.

462

463 Unequivocally identifying causal relationships between disease transmission and the
464 structure of the contact network would require matching network parameters with
465 patterns of acquisition of infection as disease moves through a population. Such
466 insight will be possible by conducting a similar study in a population of Tasmanian
467 devils recently infected with DFTD. Prior to this being achieved, our study has
468 successfully shown an association between contact patterns and propensity to engage
469 in injury causing aggressive encounters. Specifically, our results strongly suggest that

470 males engaged in mate guarding during the mating season may be particularly
471 important in the transmission of DFTD, either as recipients or transmitters of
472 infection.

473

474 A lack of detailed knowledge of contact patterns is a major issue in both the
475 management of wildlife diseases and attempts to model future outbreaks. Even in
476 populations that have been well-monitored, or in cases where clinical symptoms of
477 infection are obvious, it is notoriously difficult to pinpoint incidences of disease
478 transfer (Drewe 2010; Craft 2015; Manlove et al. 2017). Where contacts or interaction
479 patterns are studied in detail, transmission rates are often found to be influenced by
480 factors including season, behavioral tendencies and temporality (Blyton et al. 2014;
481 Langwig et al. 2015; Silk et al. 2017c). These variations at the individual level are
482 important to production of accurate and realistic disease models (Craft and Caillaud
483 2011). New technologies and methodologies are allowing more detailed insights into
484 seasonal, or even daily, variations in patterns of contact between individuals (Silk et
485 al. 2017b). Highlighting these fine scale details is critical to our understanding of
486 disease spread, as it allows a closer examination of the role individuals play in
487 epidemics (Tompkins et al. 2011). Crucially, identifying specific transmission events
488 will allow the switch from creation of contact networks, to development of
489 transmission networks based exclusively on contacts that actively transmit disease
490 (Chen and Lanzas 2016). Development of such a network for DFTD will allow better
491 understanding of how this novel disease has disseminated across most of the
492 distributional range of the species and how its future spread to unaffected populations
493 might be mitigated. Similar network transitions in studies of disease outbreaks in

494 other species and communities will extend our knowledge of how these diseases
495 spread and facilitate both containment and management of potential future outbreaks.

496

497

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705 **FIGURE LEGENDS**

706

707 **Figure 1** Contact networks based on rate of associations between individual
708 Tasmanian devils during (a) mating season and (b) non-mating season. Black squares
709 represent males, while white circles represent females – node size represents how
710 many wounds an individual accumulated during the season (0 – 17 wounds). Edges
711 between nodes represent interaction rate within the dyad – the thicker the line, the
712 higher the rate of interaction between that pair of individuals.

713

714 **Figure 2** Boxplot of the number of wounds accumulated by female and male
715 Tasmanian devils over the course of the mating and non-mating periods. Lines across
716 boxes indicate medians, while box boundaries represent interquartile ranges. Whiskers
717 identify data points no more than 1.5 times the interquartile range on either side;
718 points outside the whiskers represent extreme outliers outside this range.

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726 **TABLES AND TABLE LEGENDS**

727

728 **Table 1** Results of GLMM's showing the influence of an individual Tasmanian devil's a) interactions and b) interaction partners in
729 predicting the number of bite wounds it acquires. The model number, Akaike's Information Criterion corrected for small sample sizes (AICc),
730 difference in AICc (Δ AICc), model weight (AICc Wt), cumulative model weights (Cum. Wt) and parameter estimates for model variables
731 (including standard errors) for each GLMM run on interaction patterns using a multi-model inference approach. The relative importance of each
732 variable is indicated as the sum total of the model weights across the entire model set for each variable. Only the top three models are listed,
733 unless a higher number than this fail to exceed a threshold of Δ AICc < 5.

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a)

K	AICc	Δ AICc	AICc Wt	Cum. Wt	Sex	Season	Hours O.S.	Hours S.S.	< 1min	> 1min
7	199.95	0	0.81	0.81	0.69 ± 0.21	0.04 ± 0.27	0.15 ± 0.03	—	—	—
7	203.03	3.08	0.17	0.98	0.80 ± 0.22	0.02 ± 0.28	—	—	0.06 ± 0.01	—
7	207.30	7.35	0.02	1.00	0.83 ± 0.25	-0.12 ± 0.27	—	—	—	0.20 ± 0.06
<i>Relative importance of variable</i>					1.00	1.00	0.81	0.00	0.17	0.02

b)

K	AICc	Δ AICc	AICc Wt	Cum. Wt	Sex	Season	Weak	Intermediate	Strong	Male	Female
7	203.43	0	0.93	0.93	0.80 ± 0.23	0.006 ± 0.28	—	—	0.05 ± 0.01	—	—
7	208.48	5.05	0.07	1.00	0.39 ± 0.27	-0.41 ± 0.25	—	—	—	—	0.04 ± 0.01
7	222.02	18.60	0.00	1.00	1.52 ± 0.39	0.04 ± 0.35	—	—	—	0.05 ± 0.03	—
<i>Relative importance of variable</i>					1.00	1.00	0.00	0.00	0.93	0.00	0.07

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744 **Table 2** Results of Network Autocorrelation Models run on mating and non-
 745 mating season Tasmanian devil networks. Models examined the number of wounds
 746 received as an outcome of individual sex, while also controlling for non-independence
 747 of measures to quantify the effect of network position measures of degree,
 748 betweenness, closeness and clustering coefficient.

749

750 *Mating Season*

Model term	Estimate	S. E.	Z value	P value
Intercept	- 3.702	3.197	- 1.158	0.266
Sex	6.105	2.124	2.874	0.012*
Degree	- 0.031	0.745	- 0.042	0.967
Betweenness	0.072	0.149	0.486	0.635
Closeness	34.280	22.559	1.520	0.151
Clustering Coef.	- 7.605	39.362	- 0.193	0.850

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752 *Non-Mating Season*

Model term	Estimate	S. E.	Z value	P value
Intercept	1.627	1.802	0.903	0.380
Sex	- 0.431	1.185	- 0.364	0.721
Degree	0.337	0.308	1.095	0.290
Betweenness	0.014	0.083	0.173	0.865
Closeness	21.243	14.919	1.424	0.174
Clustering Coef.	16.559	33.564	0.493	0.628

753

754 **Table 3** Mean (\pm S.E.) social network metrics for Tasmanian devils by sex and season. Values of metrics which alter significantly ($p <$
755 0.05) between females and males within seasons, and between all individuals between seasons are in bold.

Network measures	Mating season			Non-Mating Season		
	Females	Males	Both sexes	Females	Males	Both sexes
N	11	9	20	12	10	22
Wounds	3.55 \pm 0.62	9.33 \pm 2.09	6.15 \pm 1.17	2.25 \pm 0.77	1.70 \pm 0.73	2.00 \pm 0.53
Degree	7.36 \pm 0.73	7.00 \pm 1.05	7.20 \pm 0.61	7.58 \pm 1.07	9.10 \pm 1.16	8.27 \pm 0.78
Betweenness	14.25 \pm 4.38	12.62 \pm 4.90	13.52 \pm 3.18	13.05 \pm 3.14	16.45 \pm 4.67	14.59 \pm 2.68
Closeness	0.019 \pm 0.0009	0.019 \pm 0.001	0.019 \pm 0.0007	0.012 \pm 0.0008	0.013 \pm 0.0005	0.012 \pm 0.0005
Clust. Coef.	0.48 \pm 0.04	0.40 \pm 0.06	0.44 \pm 0.04	0.64 \pm 0.06	0.54 \pm 0.05	0.60 \pm 0.04

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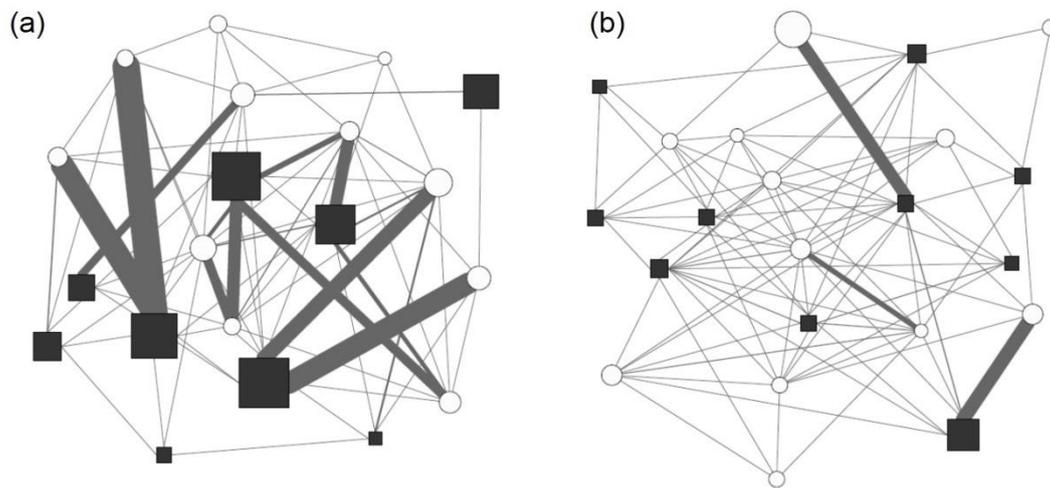
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762 **FIGURES**

763

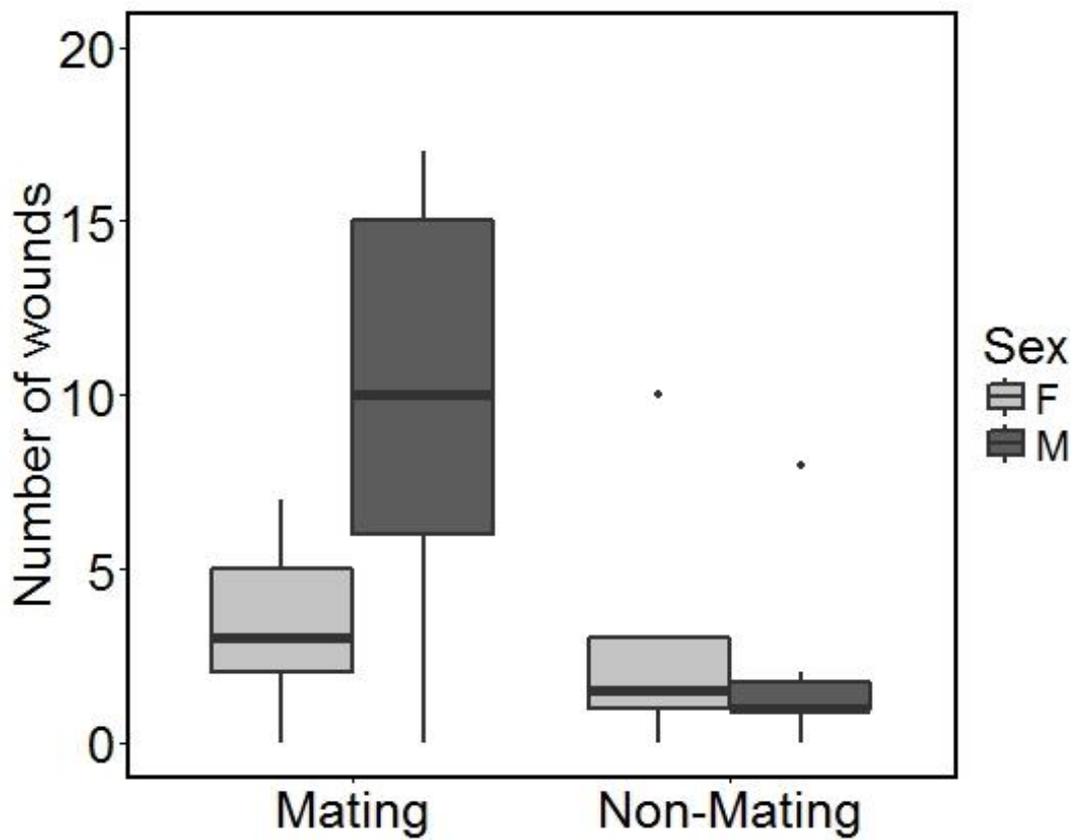
764 **Figure 1**



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767 **Figure 2**



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