



Original Article

Rate of intersexual interactions affects injury likelihood in Tasmanian devil contact networks

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Identifying the types of contacts that result in disease transmission is important for accurately modeling and predicting transmission dynamics and disease spread in wild populations. We investigated contacts within a population of adult Tasmanian devils (*Sarcophilus harrisii*) over a 6-month period and tested whether individual-level contact patterns were correlated with accumulation of bite wounds. Bite wounds are important in the spread of devil facial tumor disease, a clonal cancer cell line transmitted through direct inoculation of tumor cells when susceptible and infected individuals bite each other. We used multimodel inference and network autocorrelation models to investigate the effects of individual-level contact patterns, identities of interacting partners, and position within the social network on the propensity to be involved in bite-inducing contacts. We found that males were more likely to receive potentially disease-transmitting bite wounds than females, particularly during the mating season when males spend extended periods mate-guarding females. The number of bite wounds individuals received during the mating season was unrelated to any of the network metrics examined. Our approach illustrates the necessity for understanding which contact types spread disease in different systems to assist the management of this and other infectious wildlife diseases.

Key words: contact network, disease transmission, infectious cancer, social network analysis, social behavior, Tasmanian devil facial tumor disease, transmission event.

INTRODUCTION

Emerging infectious diseases (EIDs) are a major threat to biodiversity globally (De Castro and Bolker 2005; Smith et al. 2006). EIDs frequently impact populations that are already declining, thereby exacerbating the effects of habitat degradation, pollution, human–wildlife conflict or climate change (Blaustein et al. 2011; Heard et al. 2013). An increasing number of EIDs are recognized to cause severe population declines, including 2 species of chytrid fungus in amphibians (Stuart et al. 2004; Martel et al. 2014) and white-nose syndrome in bats (Blehert et al. 2009). The transmission processes by which infectious diseases spread through natural populations

are not well understood, but their dynamics are underpinned by the behavior of individuals. Evaluating how contact patterns affect the transmission dynamics of infectious diseases within and among populations is an urgent priority for management of infectious disease and endangered species conservation.

Patterns of interaction among individuals have major consequences for disease dynamics of directly transmitted pathogens, including transmission, and the rate and spatial scale of spread (Kappeler et al. 2015; Arthur et al. 2017). In highly social species, such as group-living mongooses (Drewe 2010) and most primates (MacIntosh et al. 2012; Carne et al. 2014), individuals associate closely within social groups and groups interact regularly, often in territorial conflicts or out-breeding events (Madden et al. 2009; Weber et al. 2013). Regular interaction between group members facilitates rapid disease spread within groups, while

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intergroup contacts allow disease spread among groups and between populations (Craft et al. 2011). Patterns of disease transmission are more varied in solitary species, where interactions between individuals are less frequent, and the extent of the effect can be influenced by population size and density (Caillaud et al. 2006; Langwig et al. 2012). In solitary species, spread of pathogens (particularly those requiring direct contact for transmission) generally occurs during specific events, such as mating (Ganguly et al. 2016) or competition over resources (Wright and Gompper 2005). In these cases, the familiarity of individuals may influence the likelihood of a successful transmission event (Vander Wal et al. 2012; VanderWal et al. 2016; Hasenjager and Dugatkin 2017). For example, familiar individuals may have an established dominance hierarchy that seldom requires physical interaction. Consequently, unfamiliar individuals may be more likely to have physical confrontations (Brunton et al. 2008; Robinson et al. 2015), thereby heightening the chance of pathogen transfer. Thus, identifying the circumstances under which transmission is likely to occur is important for understanding disease dynamics, but can be difficult in cryptic species.

Social network analysis is increasingly used as a tool for understanding process flows through biological systems (Krause et al. 2007; Aplin et al. 2015; Craft 2015; Silk, Croft, Delahay, Hodgson, Boots, et al. 2017; White et al. 2017) as it facilitates analysis of how contact patterns at the individual level, and network structures at the population level, influence transmission dynamics (Rushmore et al. 2013; Rimbach et al. 2015). Studies of information transfer (e.g., discovery of resource patches, novel foraging methods) have revealed patterns relating to networks both within and between species, and how these affect information flow (Aplin et al. 2012; Farine et al. 2012; Aplin et al. 2015; Firth et al. 2016). Emerging patterns that link an individual's centrality (the various properties of its position in a community; Borgatti 2005) within a network to its influence on transmission dynamics have been uncovered in multiple processes, particularly information flow (Aplin et al. 2012; Allen et al. 2013), parasite load (Godfrey et al. 2010; VanderWal et al. 2014), and disease spread (Drewe 2010; Weber et al. 2013; Silk et al. 2018). Key metrics relating to transmission include *degree* (representing either the total number of interactions individuals have, or the total number of other individuals they interact with), *betweenness* (number of shortest paths between nodes in the network that flow through an individual), and *clustering coefficient* (probability that an individual's neighbors are also well connected). For example, individuals that regularly engage in behaviors involving direct interactions (e.g., mate prospecting, grooming) will have high scores for degree metrics, while individuals that act as bridges between disparate groups are easily identifiable by high betweenness (Weber et al. 2013). Both tendencies inflate risk of pathogen transmission (Drewe 2010; MacIntosh et al. 2012), and can play key roles in transmission dynamics. In extreme cases, such individuals can be superspreaders (Lloyd-Smith et al. 2005) responsible for the majority of infections in a population, and thus those that are particularly important to identify as potential targets for intervention.

The Tasmanian devil (*Sarcophilus harrisii*) and its transmissible cancer, devil facial tumor disease (DFTD), provide an excellent study system to quantitatively assess infection risk using contact networks. Devils are under threat from DFTD, which is transmitted when live tumor cells, the pathogenic agent (Pearse and Swift 2006), are transferred from infected to susceptible individuals when they bite one another (Hamede et al. 2013). Individuals that develop DFTD almost invariably die within 6–12 months of clinical symptoms appearing (Loh et al. 2006; Hamede et al. 2012; Wells et al. 2017).

The key to understanding the transmission dynamics of DFTD and modeling its spread is establishing the patterns of contact that result in bite wounds (Hamede et al. 2013). In devils, the most common type of contacts, such as those between individuals with overlapping home ranges (Guiler 1970) and at regular aggregations around food sources (Pemberton and Renouf 1993), are most likely to be benign with little or no injurious biting. However, observing interactions that may be linked to disease spread is difficult since devils are cryptic and nocturnal, with some behaviors linked to injuries (such as mating) occurring in their underground burrows. Using proximity loggers (radio-collars capable of logging when individuals come in close proximity) to investigate contact networks in wild devils, Hamede et al. (2009) found that all devils in a population were connected in a single network and that contact frequencies were higher during the mating season, but the relationship between contact rates and the likelihood of being bitten was not assessed.

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

MATERIALS AND METHODS

Proximity loggers

We used proximity data loggers fitted to adjustable collars (Sirtrack E2, Havelock North, New Zealand) to record interactions between devils. Each logger emits a unique UHF pulse so that when 2, or more, loggers are within a predetermined distance of one another (calibrated via UHF detection range) the time, date, encounter length and unique logger number(s) are recorded and stored on the devices internal memory. Collars also incorporated a VHF component, on a separate circuit and battery, so the animals could be located. The entire collar assembly weighed 120 g—less than 2.5% of the body weight of the smallest individual collared.

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

Upon collar retrieval, data from each individual were filtered to ensure that there was symmetry between collar data for each dyad. For all interactions greater than 1 s that were logged by both collars in a dyad we took the time between when the first collar

commenced logging and when the last collar terminated logging as the interaction duration. Contacts of 1 s duration were eliminated from the dataset, as these represent “phantom contacts”—the result of collars being just outside detection range and incorrectly decoding faint signals as contact events (Prange et al. 2006).

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

Study site and data collection

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

Tasmanian devils were caught for collaring by setting 35 traps over a 25 km^2 area for a period of 1 month. Traps were custom built of 300 mm polypipe and baited with a variety of meats. The population of devils used for the study had been surveyed regularly for 2 years prior; therefore, we had previous knowledge of which individuals were resident and which were vagrants (see Supplementary Material 2 for details of the background population). All sexually mature devils (2 years of age and older) trapped in the study area with a trap history that indicated they were residents of the core area were fitted with collars between January and March 2015 (12 females, 10 males). Geographical barriers to the south (the deep and 20–100 m wide Arthur River), east (wide tracts of open paddock), and west (the Indian Ocean) limit movement of new adult individuals into the population. Proximity collars were activated and collecting contact data on devils from January until the end of June 2015. This timespan encompasses both mating (February to April) and nonmating periods (May to June), so differences in contact rates between reproduction-relevant seasons could be assessed, with 22 animals available for the nonbreeding season and 20 in the breeding season. The timing of the mating season was determined by backdating birth date and pregnancy based on the developmental stage and size of pouch young (see Hesterman et al. 2008; Hamede et al. 2009 for further details).

Collared devils were retrapped monthly throughout the study period to document new wounds as they occurred, as well as to assess collar fit. Only wounds that penetrated the dermis were recorded, as these are the injuries that have the potential to result in DFTD transfer. The period between captures of each individual was generally a month or less, meaning that new wounds were unlikely to have healed between captures (penetrating wounds in Tasmanian devils take 3–8 weeks to heal to a point at which they are undetectable, depending on their severity). Positions of wounds on the animal were recorded and photographed on each capture so that new

wounds could be identified on future captures (see Supplementary Material 3 for examples). Since agonistic interactions with other predators (spotted-tailed quolls, *Dasyurus maculatus*, and feral cats, *Felis catus*) are extremely rare (Jones 1995), all wounds recorded are likely to have come from conspecifics.

Network construction and statistical analyses

Contact networks were constructed in the *igraph* package in R v3.2.5 (R Core Team 2018) using the filtered contact rate in each dyad. Networks were separated into mating (15th February to 15th April) and nonmating (January to 15th February and 15th April to 30th June) seasons. Individuals were represented as nodes linked by observed contact rates. The size of nodes represented the number of wounds individuals received over the course of each season, while lines between nodes (edges) were weighted by the rate of contacts. Network metrics and properties (detailed later) were also calculated using *igraph*.

We investigated the relationship between individual interactions and the number of wounds that devils accumulated over the course of the study for all 22 devils in the adult population. We used generalized linear mixed models (GLMMs) with Poisson error to assess the effects of the number of bite wounds on 2 categorical variables (sex and season) and 4 continuous variables describing modes of interactions: 1) rate of interactions of less than 1 min, 2) rate of interactions of more than 1 min, 3) proportion of hours spent in extended pairings with opposite sex, and 4) proportion of hours spent in extended pairings with the same sex. Interactions totaling less than 1 min represent brief contacts, where individuals come into close proximity for a short period, while interactions totaling more than 1 minute represent prolonged interactions. The hours spent in extended pairings with the opposite sex represent 2 devils sharing a den in close proximity. Regular physical confrontation can occur during these periods, which last from 1 to 13 days as males attempt to restrain females from departing during their estrous. Hours spent in extended pairings with the same sex represent intrasex den sharing—it is likely that these events represent devils tolerating each other's presence, although physical aggression could occur during such encounters. To account for small sample size ($n = 22$ individuals over 2 seasons), we included no more than 3 independent variables per model and no more than 5 models in each analysis. Based on a priori knowledge (Hamede et al. 2013), and clear patterns in the results, that 1) devils acquire more wounds in the mating season, and 2) males acquire more wounds than females (Figure 2), the categorical variables accounting for sex and season (and an interaction term between them) were retained in the majority of the models. Each model contained 1 random factor, individual, to account for the models including data separated into seasons (mating and nonmating) for each individual. The null model contained only the random factor.

We developed model hypotheses related to the factors potentially influencing biting contacts (and therefore potential transmission of DFTD) in devils, to derive the best prediction of the number of bite wounds an individual received over the course of the mating and nonmating seasons. We used a multimodel inference approach (Burnham and Anderson 2002), ranking models using Akaike's Information Criterion corrected for small sample size (AICc). All models were run using the *lme4* and *AICmodavg* packages in R v3.2.5 (R Core Team 2018). See Supplementary Material 4 for a list of all models run.

We then investigated the relationship between the identity of an individual's interaction partners and the number of bite wounds it

received in a further set of GLMMs (using the same multimodel inference approach and packages as detailed above). For this analysis, we measured the effect of the regularity with which an individual interacted with their dyadic partners, as well as the sex of those dyadic partners, on the number of bite wounds they received. To quantify the regularity of contact with interaction partners, each dyad was ranked as “weak” (rate of 0 to 0.1 interactions per day), “intermediate” (rate of 0.1 to 0.5 interactions per day), or “strong” (rate of > 0.5 interactions per day) ties. These represent the regularity of contact between pairs of individuals and may affect likelihood of involvement in a physical interaction with one another. Analyses were run using both more and less generous cut-off frequencies for “weak” (rate of 0.05 through 0.4 per day), “intermediate” (rate of 0.05 through 1 per day), and “strong” (0.5 through 2 or more per day) dyads, but patterns remained identical at the varying thresholds. The dyadic ranking thresholds used in the final models divide the observed data into 3 approximately equal groups. We assessed the effects of 2 categorical variables (sex and season) and 5 continuous variables (rate of interactions in “weak” dyads, rate of interactions in “intermediate” dyads, rate of interactions in “strong” dyads, rate of interactions with males, and rate of interactions with females) on the number of bite wounds acquired by individuals. The same random factor (individual) as in the previous set of models was included in all models, including the null model.

Finally, to establish the influence of an individual’s position within a network (network metrics) on its propensity to pick up bite wounds, we applied network autocorrelation models (NAMs; R package *tnam*) to the contact networks for mating season and nonmating season, respectively. In each model, sex and age were fitted as fixed effects, while terms were fitted for social network metrics which are likely to have an influence on disease transmission, specifically: 1) weighted degree (the proportion of individuals in a population that an individual associates with); 2) betweenness centrality (the number of shortest paths that flow through a node); 3) closeness centrality (metric based on the sum of shortest paths that run through a node); and 4) clustering coefficient (measure of how many of a node’s connections are also connected). None of these network metrics were significantly correlated with one another. Each network term was centered, while the inherent nonindependence of connected individuals in the network was accounted for using a *weightlag* term in the model. All network centrality measures examined provide indications of how influential an individual will be in the event of disease spreading through a population. If these metrics relate to the number of potentially disease-causing bite wounds an individual receives, they provide a proxy for the role of that individual in DFTD transmission in the case of an

outbreak. We also tested for differences in bite wounds and social network metrics between sexes and seasons using node-permuted *t*-tests, comparing to 10,000 randomized *t*-statistics to account for nonindependence (Croft et al. 2011).

RESULTS

The total number of interactions recorded was 8854 (7126 in the mating season, 1728 in the nonmating season), and the network metrics and wounds are summarized in Table 1. The mean number of bites received per individual was 6.15 (SE = 1.17) in the mating season and 2 (SE = 0.53) in the nonmating season (Table 1). Contact networks were comprised of one large component (i.e., all individuals were connected, either directly or indirectly) during both the mating and nonmating seasons (Figure 1). The number of wounds received by devils differed significantly between seasons ($P = 0.005$; paired *t*-test), and between sexes during the mating season ($P = 0.026$), with a higher number of wounds being received by males, particularly during the mating season (Figure 2). The only network metrics which differed between seasons were closeness centrality, which was significantly higher during the mating season ($P = < 0.001$), and clustering coefficient, which was significantly higher during the nonmating season, particularly in females ($P = 0.019$; Table 1).

Influence of individual interactions

The most important predictor of the number of bite wounds received was the proportion of hours an individual spent in extended intersexual contacts. This effect was sex specific. Under the single best fitting model males accrued one additional bite wound for every 42.59 h spent in extended intersexual contacts in the breeding season; no pattern was apparent for females. This model, which accounted for 81% of AICc weight, included this factor alongside the categorical variables sex and season (Table 2, a). A second model (incorporating rate of contacts of less than 1 min, sex and season) was separated from the first model by just over 3 units of AICc ($\Delta\text{AICc} = 3.08$) and accounted for 17% of AICc weight (Table 2, a). Other models had much greater steps in AICc.

Influence of interaction partners

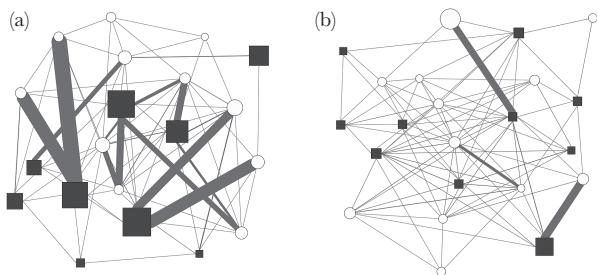
The more time male devils spent in strong dyads, the more likely they were to accumulate bite wounds. The best supported model in the analysis of influence of dyad partners contained the factors strong ties (interaction rate of > 0.5 per day), sex and season, and accounted for 93% of AICc weight (Table 2, b). A second model, explaining 7% of AICc weight ($\Delta\text{AICc} = 5.05$), contained the

Table 1

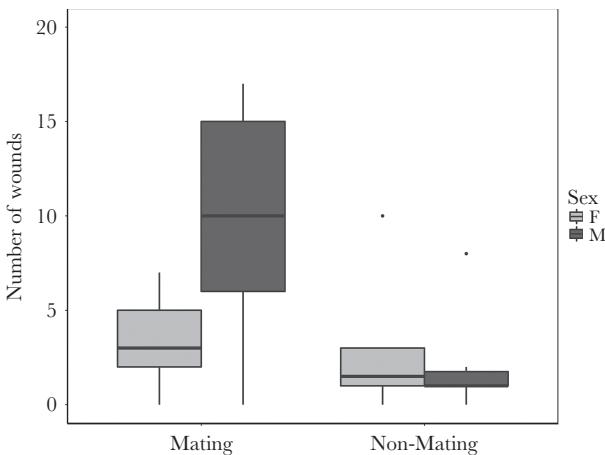
Mean (\pm SE) social network metrics based on interaction rates for Tasmanian devils by sex and season

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

Values of metrics which alter significantly ($P < 0.05$) between females and males within seasons, and between all individuals between seasons are shown in bold.

**Figure 1**

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

**Figure 2**

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

number of contacts with female interaction partners. The models containing weak and intermediate ties received no support (Table 2, b).

Influence of network position

None of the network metrics examined provided a strong predictor of the number of bite wounds an individual received. The only factor found to influence number of bite wounds accrued was the sex of the individual, again with males more likely to obtain bite wounds in the mating season (Table 3). Similarly, none of the network metrics examined proved to be a strong predictor of the number of bite wounds accrued in the nonmating season (Table 3).

DISCUSSION

Identification of potential disease transmission events, and their occurrence within contact networks, is critical for understanding the dynamics of disease spread (Craft 2015; Chen and Lanzas 2016; Manlove et al. 2017). Here, we conducted a contact network study

in Tasmanian devils while simultaneously examining potential disease transmission events. Divergences between sexes and seasons were identified which are likely to have significant consequences for the spread of disease in Tasmanian devils. Males acquired more dermis-penetrating bite wounds with the potential to facilitate DFTD transmission than females, and these occurred mostly during the mating season. Acquisition of bite wounds in males was highly correlated with time spent in extended contacts with females, particularly those with whom they interacted regularly. These results contribute to our understanding of disease susceptibility and how it relates to variations in contact patterns between individuals (Altizer et al. 2006; Blyton et al. 2014; Han et al. 2015).

Our use of proximity loggers indicated that the mating season wounds received by males were associated with extended associations with females (lasting 1–13 days), shedding doubt on a previously held perception that the large number of injuries in males during the mating season result from male–male combats aimed at accessing females (Hamede et al. 2008). Mate-guarding behavior is seen in devils (Jones, unpublished data) and a variety of other species (Taggart et al. 2003), and involves males attempting to exclude other males from access to a female in estrus to increase the guarder's chance of paternity. Guarding behavior can involve high levels of aggression towards competing males (Girard-Buttoz et al. 2014; Baxter et al. 2015), and can also be associated with aggression between the male and the female being guarded (Elias et al. 2014), including in devils (Jones, unpublished data). However, male–male interactions were rare during the mating season and their rate of occurrence was not associated with frequency of injuries. This result corroborates the findings of Hamede et al. (2009) that devil mixing patterns during the mating season were almost entirely intersexual. Our additional examination of the bite wounds devils accrued whilst involved in interactions with other devils has allowed insights into the potential of these associations to result in disease transfer. Our results suggest that males are being wounded while guarding females in estrus, and the longer they spend engaged in this type of behavior, the more wounds they receive. This highlights the potential for mating interactions to enhance disease transmission, and is consistent with recent findings that Tasmanian devils with a high reproductive output are more likely to contract DFTD during their lifetime (Wells et al. 2017). Use of proximity collars has provided new insights into the mating behavior of devils, a cryptic, nocturnal species that is difficult to observe directly in the wild, particularly mating interactions that usually occur in underground burrows.

Network structure and contact rates between devils were comparable with a previous study (Hamede et al. 2009). In both studies, networks for the mating and nonmating seasons were comprised of one large component, male–male interactions were relatively rare and extended male–female interactions made up the bulk of contacts during the mating season. While values for degree and betweenness were higher in the 2009 study (see Hamede et al. 2009 and Table 1), network density was comparable, indicating divergences can likely be attributed to the higher number of nodes in the earlier networks. This suggests that large-scale patterns observed in devil networks, particularly pertaining to the mating interactions that are potentially critical to disease transfer, are relatively consistent between populations.

Given that a high proportion of potentially disease-transmitting bite wounds occurred during the mating season, particularly during mate guarding, how does this compare to observations of patterns of the transmission of DFTD? Unfortunately, the disease

Table 2

Results of GLMM's showing the influence of an individual Tasmanian devil's (a) interactions and (b) interaction partners in predicting the number of bite wounds it acquires

| | K | AICc | ΔAICc | AICc Wt | Cum. Wt | Sex | Season | Hours O.S. | Hours S.S. | < 1min | > 1min | |
|--|---|--------|-------|---------|---------|-------------|--------------|-------------|--------------|-------------|-------------|-------------|
| a) | 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 | |
| Relative importance of variable | | | | | | | 1.00 | 1.00 | 0.81 | 0.00 | 0.17 | 0.02 |
| | K | AICc | ΔAICc | AICc Wt | Cum. Wt | Sex | Season | Weak | Intermediate | Strong | Male | Female |
| b) | 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 | — |
| Relative importance of variable | | | | | | | 1.00 | 1.00 | 0.00 | 0.93 | 0.00 | 0.07 |

The model number, Akaike's Information Criterion corrected for small sample sizes (AICc), difference in AICc (ΔAICc), model weight (AICc Wt), cumulative model weights (Cum. Wt) and parameter estimates for model variables (including standard errors) for each GLMM run on interaction patterns using a multimodel inference approach. The relative importance of each variable is indicated as the sum total of the model weights across the entire model set for each variable. Only the top 3 models are listed, unless a higher number than this fail to exceed a threshold of ΔAICc < 5.

Table 3

Results of Network Autocorrelation Models run on mating and nonmating season Tasmanian devil networks

Mating Season

| Model term | Estimate | SE | 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 |

Nonmating Season

| Model term | Estimate | SE | 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 |

Models examined the number of wounds received as an outcome of individual sex, while also controlling for nonindependence of measures to quantify the effect of network position measures of degree, betweenness, closeness, and clustering coefficient.

does not have a consistent latent period, with the limited information available on time from transmission event to development of clinical signs ranging from 3 weeks (in experimental trials) to 11 months in the wild (asymptomatic individual developing tumors after being brought into captivity). This variability in latent period obscures any potential seasonality in the transmission of the disease (Hamede et al. 2009; McCallum et al. 2009). Additionally, there is no evidence from extensive mark-recapture data that DFTD prevalence differs between the sexes (Hawkins et al. 2006;

McCallum et al. 2009; Hamede et al. 2012, 2013). This lack of sex bias in disease prevalence seems to contradict our results, which indicate that males are more likely to obtain potentially disease-transmitting wounds. However, most injuries to males were associated with their interaction rate with females rather than males, which supports a lack of sex bias in disease prevalence. Outside of the mating season, the rate of biting injuries and most network metrics are more even between the sexes and the rate of injurious biting is lower than that during the mating season. However, cumulatively over the course of the year the number of injuries is still substantial and likely to have an influence on DFTD transmission. Notably, both sexes display heightened levels of clustering (meaning they are well connected to other well-connected individuals within the network; see Figure 1 and Table 1) outside the mating season, which may increase their probability of coming into contact with diseased individuals (even though their total number of potentially disease-causing interactions is lower). This additional potential for exposure to diseased individuals outside the mating season would result in DFTD continuing to spread through the population even during periods when the seemingly critical mating interactions are not occurring. Further studies of the contact patterns of devils in DFTD-affected populations are required to identify additional vulnerable periods throughout the year and to fully explain the lack of sex bias observed in DFTD prevalence.

In terms of relating our findings to real time transmission of DFTD in the wild, there is uncertainty concerning the dominant direction of disease transfer. Transmission could occur by devils biting the tumor of another animal, or by having live tumor cells inoculated when they are bitten. Empirical data support the former possibility, as devils that have fewer bite wounds are more likely to acquire the disease (Hamede et al. 2013). This led to the hypothesis that more dominant animals were biting subordinate animals, possibly into their tumors, and becoming infected (Hamede et al. 2013), which appears consistent with results suggesting individuals with higher reproductive success were more likely to acquire DFTD (Wells et al. 2017). The results presented here, and observations of devil mating behavior in captivity (Jones, unpublished data), suggest that both

sexes bite each other during mating interactions, but females cause a higher number of injuries (to the males) during the mating season, when there is also an annual peak in biting injuries (Hamede et al. 2013). Insights into cryptic devil behavior are beginning to overturn our assumptions about male dominance in aggressive encounters and suggest that males could be critical to transmission dynamics during the mating season, as they are involved in high numbers of interactions as either the potential vector or recipient of DFTD cells. However, it remains unclear what proportion of transmission incidences result from biting or from being bitten. A combination of both forms of transmission would reconcile the lack of sex bias in DFTD prevalence with our results. Further understanding of the directionality of disease transfer is required before we can fully ascertain how DFTD travels through devil populations.

Unequivocally identifying causal relationships between disease transmission and the structure of the contact network would require matching network parameters with patterns of acquisition of infection as disease moves through a population. Our conclusions are based on the behavior of Tasmanian devils that are disease-free, but disease infection may alter behavioral contacts, and alter transmission pathways. Both short-term behavioral changes resulting directly from symptoms of infection and long-term changes due to differential survival of more or less interactive individuals are possible. Therefore, such insight will be possible only by conducting a similar study in a population of Tasmanian devils recently infected with DFTD. Prior to this being achieved, our study has successfully shown an association between contact patterns and propensity to engage in injury causing aggressive encounters. Specifically, our results strongly suggest that males engaged in mate guarding during the mating season may be particularly important in the transmission of DFTD, either as recipients or transmitters of infection.

A lack of detailed knowledge of contact patterns is a major issue in both the management of wildlife diseases and attempts to model future outbreaks. Even in populations that have been well monitored, or in cases where clinical symptoms of infection are obvious, it is notoriously difficult to pinpoint incidences of disease transfer (Drewe 2010; Craft 2015; Manlove et al. 2017). Where contacts or interaction patterns are studied in detail, transmission rates are often found to be influenced by factors including season, behavioral tendencies, and temporality (Blyton et al. 2014; Langwig et al. 2015; Silk, Weber, et al. 2017). These variations at the individual level are important to parameterize accurate and realistic disease models (Craft and Caillaud 2011). New technologies and methodologies are allowing more detailed insights into seasonal, or even daily, variations in patterns of contact between individuals (Silk, Croft, Delahay, Hodgson, Weber, et al. 2017). Highlighting these fine-scale details is critical to our understanding of disease spread, as it allows a closer examination of the role individuals play in epidemics (Tompkins et al. 2011). Crucially, identifying specific transmission events will allow the transition from creating contact networks, to developing transmission networks, based exclusively on contacts that actively transmit disease (Chen and Lanzas 2016). Development of such a network for DFTD will allow better understanding of how this novel cancer has disseminated across most of the distributional range of the species and how its future spread to unaffected populations might be managed. Similar network transitions in studies of disease outbreaks in other species and communities will extend our knowledge of disease ecology as well as improving the containment and management of potential future outbreaks.

SUPPLEMENTARY MATERIAL

Supplementary materials are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Hamilton et al. (2019).

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