Seasonal, demographic and density-related patterns of contact between Tasmanian devils (*Sarcophilus harrisii*): Implications for transmission of devil facial tumour disease

RODRIGO K. HAMEDE,* HAMISH MCCALLUM AND MENNA JONES
School of Zoology, University of Tasmania, Hobart, Tasmania, Australia
(Email: rkhamede@utas.edu.au)

Abstract Devil facial tumour disease (DFTD), is an emerging infectious cancer thought to be spread by biting. It is causing ongoing, severe population decline of the Tasmanian devil (*Sarcophilus harrisii*), the largest surviving marsupial carnivore and there are concerns that DFTD may lead to extinction of the devil. Whether extinction is likely depends on contact rates and their relationship to host density. We investigated contact rates using two different datasets. The first consisted of field observations of contact and biting behaviour around prey carcasses and, the second was a 3-year longitudinal series of injuries in a marked devil population. During feeding interactions at carcasses, contact rates were significantly positively associated with population density and subadults delivered more bites than adult males and females. Injuries from the marked devil population did not differ between adult males and females. In two of the three years, penetrating biting (resulting in injury) increased markedly during the mating season and was more frequent in adults than in subadults. Among injured devils with wounds penetrating the dermal layer, adults were more frequently bitten in the head (the location of primary tumours) in the mating season than in other seasons, and had more head bites than subadults. Our results suggest that the mating season may be the key period for disease transmission. If most penetrating bites occur during mating interactions, DFTD transmission is likely to be frequency dependent, which means that there would be no threshold host density for disease persistence, and disease-induced extinction is possible.

Key words: contact pattern, disease transmission, emerging disease, population demography, Tasmanian devil facial tumour disease.

INTRODUCTION

Emerging infectious diseases in wildlife are increasingly being recognized as serious threatening processes in conservation biology (Daszak *et al.* 2000; Lafferty & Gerber 2002; Daszak & Cunningham 2003; Macdonald & Laurenson 2006). Disease is particularly important for many mammalian carnivores, whose populations often have restricted ranges and are already impacted by habitat destruction or fragmentation, overexploitation of their prey or persecution (Murray *et al.* 1999; Funk *et al.* 2001; Woodroffe *et al.* 2004). Furthermore, loss of top predators from a system can cause trophic cascades with severe knock-on effects for populations of other carnivores, herbivores and vegetation communities (Pace *et al.* 1999; Schmitz *et al.* 2000).

To effectively manage disease threats, a good understanding of the social ecology of host species and the epidemiology of the disease is critical. Key to understanding the dynamics of directly transmitted diseases

is the relationship between frequency of contacts and population density. Similarly, the influence of seasonal, life history and reproductive events on patterns of contact is important to interpret disease dynamics and design disease control strategies (Altizer *et al.* 2004; 2006; Hosseini *et al.* 2004).

Devil facial tumour disease (DFTD) is a recently emerged disease that is causing major population decline in the Tasmanian devil (*Sarcophilus harrisii*) (Hawkins *et al.* 2006; McCallum *et al.* 2007). DFTD, a consistently fatal infectious cancer, kills within months of development of a tumour and affects mainly adults (Hawkins *et al.* 2006). Transmission trials (Pyecroft *et al.* 2007) and cytogenetic work (Pearse & Swift 2006) have confirmed that the disease is transmitted as an infectious cell line (an allograft). The only other known cancer with a similar mode of transmission is canine transmissible venereal sarcoma (Das & Das 2000; Murgia *et al.* 2006). In the 11 years since 1996, when DFTD-like symptoms were first reported, the disease appears to have spread to over 59% of the devil's distributional range, and has been associated with an overall population decline of 53% with up to 89% declines in local populations (McCallum *et al.*

2007). Formerly common, devils are now listed as Vulnerable on State and Federal Threatened Species Lists (Tasmanian Threatened Species Protection Act 1995; Commonwealth Environment Protection and Biodiversity Control Act 1999). Ongoing decline in affected areas has given rise to concerns of possible local or regional extinctions in the wild (Jones *et al.* 2007; McCallum *et al.* 2007).

In the absence of any effective treatment or vaccine, management strategies for controlling the disease in wild populations are limited. Options available include translocation of uninfected wild animals to islands, removal of infected individuals in an attempt to suppress disease and strategies to reduce the rate of transmission in the wild through behavioural or habitat modification (McCallum & Jones 2006; Jones *et al.* 2007). Whether the disease is likely to lead to local or regional extinction or whether it will 'fade out' once devils become sufficiently rare depends critically on how strongly transmission depends on population density (McCallum & Dobson 1995).

Transmission of directly transmitted diseases is usually directly proportional to population density. There is a threshold host density, below which the disease is unable to maintain itself in the host population. This result has led to the generalization that infectious diseases with only a single host are unlikely to drive that host to extinction (de Castro & Bolker 2005). Many diseases, however, have transmission that depends on the frequency of infected individuals in the population, rather than on their density (McCallum *et al.* 2001). In such cases, there is no threshold population density for disease maintenance and a single host pathogen therefore can drive its hosts to extinction. Frequency dependent transmission is common in sexually transmitted diseases because the rate of sexual contact depends weakly, if at all, on population density.

Understanding of the transmission dynamics of this disease is therefore critical in determining whether or not the disease is likely to lead to local or regional extinction. Further, evaluating potential control strategies requires the building of epidemiological models with which to assess alternative management actions. The transmission dynamics of a disease are obviously a crucial component of any epidemiological model and are usually some of the most difficult components of the disease dynamics to quantify adequately. Unfortunately, directly determining whether transmission is frequency or density dependent is surprisingly difficult from observable field data for any disease (McCallum *et al.* 2001). Often, indirect inference is the only possible approach. As well as understanding how transmission rate scales with population density, it is important to identify 'who acquires infection from whom'. In many diseases, certain age or sex classes (e.g. Ferrari *et al.* 2004) or individuals, known as

'superspreaders' are particularly important in disease transmission (Lloyd-Smith *et al.* 2005). If devils follow this pattern then any control strategy needs to be targeted at those individuals.

As devils bite and injure each other during feeding, social and mating interactions and the tumours ulcerate and become friable as they grow larger, biting is the most plausible route for transmission. Other modes of transmission, such as devils scavenging other devils that have died from disease or transfer of tumour cells from co-feeding on prey carcasses, cannot be discounted. Existing data on biting contacts between devils have elucidated issues of communication, dominance and social feeding at carcasses (Pemberton & Renouf 1993; Jones 1995; 1998), but these studies did not address the influence of seasonal variation or population density on contact rates. Contact rates traditionally have been difficult to estimate owing to the logistical constraints of making direct observations of social interactions in wild animals. Devils can be observed from a vehicle or hide at night feeding on carcasses placed in their habitat. Although this is artificial, it is a very close representation of the natural social and behavioural ecology of devils.

In this study, we used two different datasets, each with its own advantages and limitations; first, to determine how contact rate scales with population density and second, to investigate the pattern of biting contacts in relation to individual age and sex, and seasonal life history and reproductive events.

METHODS

Contact rate and population density

We collected data over a single year on contacts during social feeding interactions at seven sites across Tasmania, representing a range of population densities. This dataset has the advantage that we were able to directly observe interactions at sites with different population densities. It is limited in that we were only able to observe social feeding interactions, not sexual interactions or aggressive interactions away from the food source.

Carcasses of medium-sized, road-killed prey species (wombats, *Vombatus ursinus tasmaniensis*, Bennett's wallabies, *Macropus rufogriseus* and Tasmanian pademelons, *Thylogale billardierii*) were secured using short metal stakes in devil habitat before dark. The observer and data recorder sat in a vehicle or hut 20–25 m from the carcass, where they operated a dimmer switch controlling white lights (a set of two car reversing lights run off two 12V car batteries) set to illuminate the carcass from above. The observer watched the devils continuously and events were directly recorded onto data

sheets. Observations were made using Winchester 10×50 binoculars and a monoscope. Lights were kept off until the first devil arrived, to preclude inhibition in approaching the carcass. A one-way radio alerted the observer to the presence of a devil at the carcass. Lights were switched on briefly at low-to-medium illumination for identification of sex, age and individual markings. Once there were two or more devils on the carcass, the lights were then switched back on so that interactions could be recorded. The lights seemed to have no effect on the behaviour of feeding devils, which were by then preoccupied with feeding and contesting the carcass. All data were collected in the winter of 2004 between April and August. Observations were made continuously from dusk to dawn. Night length during this period ranged from 11 to 13 h.

The time of every arrival and departure of an individual from the carcass was recorded, allowing recording both of devils that fed at the same time and very close to each other but without any physical contact, and those that fed on the same carcass on the same night but not necessarily at the same time. Co-feeding on a carcass opens the possibility of transferring tumour cells (or pathogens) between devils via saliva and open wounds. Biting contact was scored when one devil made physical contact with another with a lunge and quick closure of the attacker's mouth on the recipient's body. Direct contact of this kind provides the greatest potential for inoculation of tumour cells. For every bite observed, the individual biter and bitten were identified, as was the location of the bite on the recipient's body. The time and population class of both individuals involved in the bite were also recorded. It was not possible to record whether these physical contacts resulted in perforation of the skin. Biting bouts, rather than separate bites, were the sample unit: multiple bites in close succession were counted as a single bite.

Individuals were identified using sketches of their unique patterns of white markings and other identifying characteristics (e.g. mange, scars). Each night (carcass) was the unit of sampling; all individual devils observed in each night were considered as new individuals. Individual devils were categorized into three population classes based on body size and sexual characteristics: adult male, adult female and subadult. The sex of subadults could not be distinguished under these field conditions. Adult males are larger, and have a massive head and broader neck compared with adult females. Both adult males and adult females are noticeably larger than subadults. In addition, subadults do not show the fur loss on the jowls and head that distinguish adult males and adult females, and retain juvenile characteristics such as a pointed and sculptured face.

Observations of feeding contact rates were recorded at seven sites across Tasmania that were selected because they represented four categories of population density (Fig. 1): low (0–0.4 devils per square kilome-
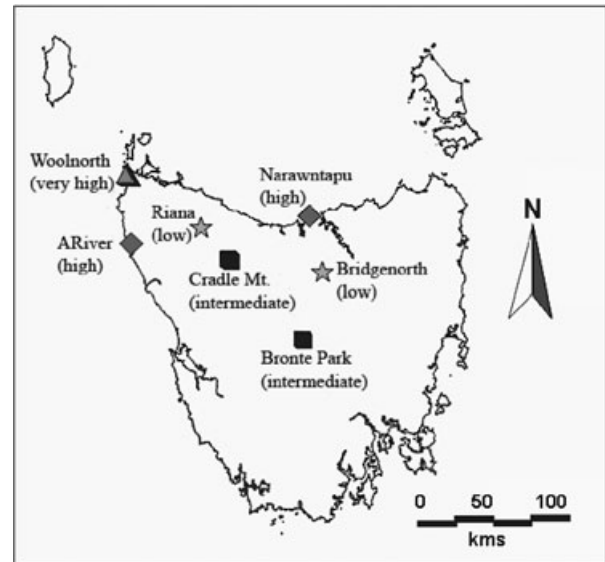
Fig. 1.   Location of study sites and densities.

tre), intermediate (05–0.9 devils per square kilometre), high (1–1.9 devils per square kilometre) and very high (>2 devils per square kilometre). These density categories were derived from previous studies and are representative of typical population densities of devils prior to DFTD (Pemberton 1990; Jones 1995; Jones & Rose 1996; Jones *et al.* 2004). Actual densities for six sites were known from previous trapping programmes. Densities for Woolnorth, Narawntapu and Bronte Park were derived from capture-mark-recapture studies conducted by the Tasmanian Government's Save The Tasmanian Devil Program (Hawkins *et al.* 2006; C. Hawkins unpubl. data 2004). Bridgenorth density was estimated from trapping results collected over a four-day period using the same protocol as the previous sites (C. Hawkins & J. Wiersma unpubl. data 2004). Densities for Cradle Mountain and Arthur River were estimated from earlier trapping studies (Jones 1995; Jones *et al.* 2004). Density for the seventh site at Riana was estimated from recent 'Devil Restaurant' activity (carcass feeding for tourists). No more than three successive nights data were recorded at the same site to minimize unnatural aggregation of the devils. Observations on successive nights at each site were conducted in different locations 10–15 km apart to maximize the number of different individuals sampled among nights and the independence of the parameter night (carcass). Devils move up to a maximum of seven kilometres on successive nights (M. Jones, unpubl. data 2002). With the exception of Bronte Park, all sites were disease free.

Demographic and seasonal patterns of injuries

To determine how the pattern of biting contact varies with individual age and sex, and seasonal life history

and reproductive events, we analysed an injury dataset that was collected regularly over a 3-year period (2000–2002) during a life history study of wild devils on 200 km² of the Freycinet peninsula on the east coast of Tasmania (M. Jones, unpubl. data 2000–2002). Devil population density at this site was medium to high at the time (prior to a major population decline caused by DFTD (Lachish *et al.* 2007)). The location on the body and the severity of all injuries on trapped devils were recorded. This dataset has the advantage of covering 3 years and different parts of the annual reproductive cycle of the population. As the animals were captured and examined, we were able to record injuries resulting from all interactions that may have occurred over an extended period. The disadvantage of this dataset is that we were not able to observe injury levels over a range of population densities.

All devils in this study were individually marked and of known age and sex. Injuries were classified according to their severity: 1 = bare patch (a small scratch or piece of fur missing but with no evidence of tooth penetration), 2 = bite (a bite or puncture where a tooth has penetrated but has left only a tooth-sized hole), 3 = small gouge (bite with penetration resulting in a hollow larger than tooth size), and 4 = piece of skin or flesh missing (bite with penetration resulting in the removal of skin or flesh). In all years, trapping trips were conducted in January, immediately before the mating season and when juveniles were being weaned and dispersing, in April immediately after the mating season, and in June–July when females were carrying large pouch young.

Statistical analysis

All analyses were performed using R version 2.4.1. The biting rate data were analysed using a REML-based linear mixed model (lmer in R package lme4), with density, site and age class as fixed effects and the observation night at each site as a random effect. Demographic and seasonal patterns of injury on the Freycinet peninsula were analysed using logistic models. The models were simplified by removing terms and combining factor levels along lines recommended by Crawley (2005). The effects of removing terms and combining factor levels are reported as χ^2-distributed likelihood ratios comparing models and the effects of individual levels of factors are reported as Wald statistics (estimate divided by standard error) for the relevant parameter.
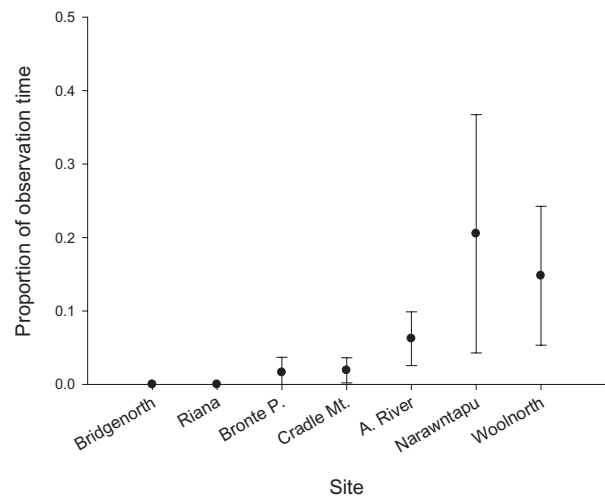
RESULTS

Contact rate and population density

A total of 481.5 h of observation were made over 47 nights, during which time 147 biting bouts were
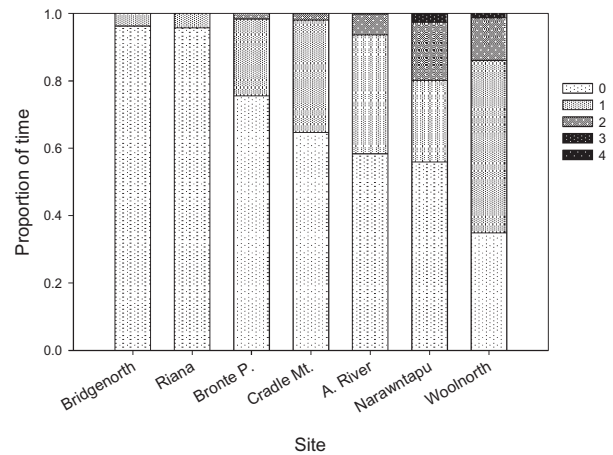
Fig. 2. The proportion of total observation time at each site for which differing numbers of devils were present. The sites are in order of increasing devil abundance.

Fig. 3. The proportion of observation time each night for which more than one devil was present at the carcass. Sites are arranged in order of increasing devil abundance and the error bars show 95% confidence intervals derived from night to night variation at each site.

recorded. Multiple devils were present at the same carcass for only a minority of the observation time, but up to four animals were observed simultaneously (Fig. 2). The proportion of time during which more than one devil was present at the carcass increased with density at the site (Fig. 3). The rate at which bites were received per hour increased with ranked devil abundance per site ($\chi^2 = 8.12$, d.f. = 1, $P = 0.004$), with marginal evidence of differences between population classes ($\chi^2 = 6.01$, d.f. = 2, $P = 0.049$; see Fig. 4a). There was also marginal evidence of differences between sites in addition to the density effect ($\chi^2 = 7.82$, d.f. = 3, $P = 0.05$). Subadults bit more frequently than the adult classes ($\chi^2 = 6.74$, d.f. = 1,
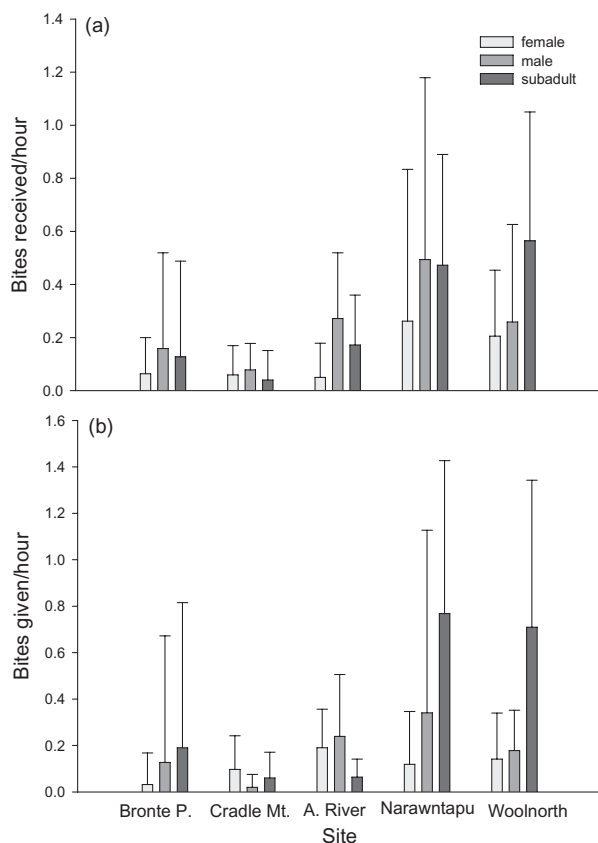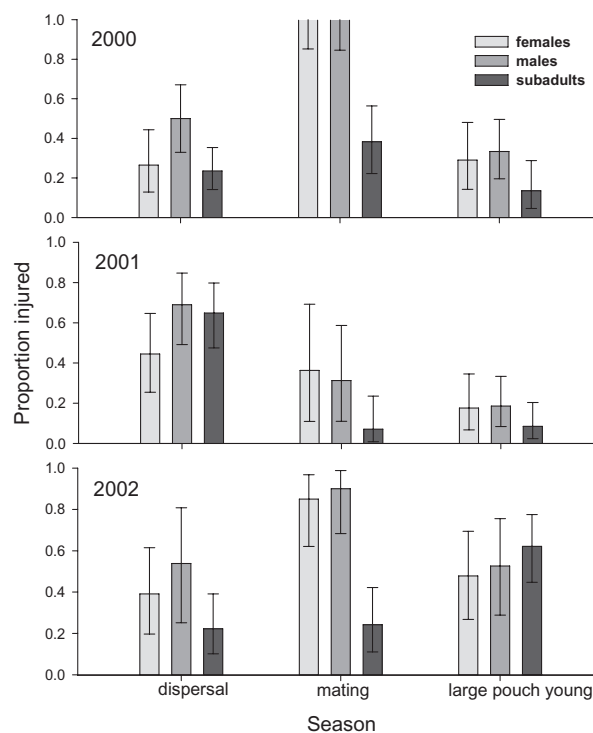
Fig. 4. The rate at which bites were received (a) and given (b) per hour at sites, arranged in order of increasing devil abundance. The error bars show 95% confidence intervals derived from night to night variation.

Fig. 5. The proportion of Tasmanian devils captured that were injured on the Freycinet Peninsula between 2000 and 2002. Observations were made at three time periods representing different life history events: 'dispersal' (January, when juveniles become independent and disperse), 'mating' (April, immediately post mating season) and 'large pouch young' (June–July, when females were carrying large pouch young). Error bars are exact binomial 95% confidence intervals.

$P = 0.009$). No additional variation was attributable to differences between males and females ($\chi^2 = 0.45$, d.f. $= 1$, $P = 0.5$; see Fig. 4b).

In each of subadults, males and females, the majority of bites were delivered to the head. Of the 147 biting bouts observed 87.8% were delivered to the head, 9.5% to the body, 2.7% to the tail and none to the limbs.

## Demographic and seasonal patterns of injuries on the Freycinet Peninsula

Significant two-way interactions in the logistic model indicated differences between population classes in the proportion of devils injured (population class by season: $\chi^2 = 49.9$, d.f. $= 4$, $P < 0.001$) and among years (year by season: $\chi^2 = 89.9$, d.f. $= 4$, $P < 0.001$). Most of these differences in injury levels between population classes were attributable to differences between adults and subadults, with a model containing all three population classes fitting only marginally better than one contrasting adults and subadults

($\chi^2 = 8.13$, d.f. $= 3$, $P = 0.043$). Inspection of Fig. 5 suggests that 2001 (in which there was a drought) might show a different pattern from the other two years. However, attempted model simplification showed that a model retaining all 3 years as separate factors fitted the data much better than one contrasting 2001 with the other two years ($\chi^2 = 24.7$, d.f. $= 3$, $P = 0.00002$).

Accordingly, we analysed the data from each year separately. In 2000, a model including all three seasons and three age classes fitted no better than a more parsimonious model contrasting the mating season *versus* the other two seasons and adults *versus* sub-adults ($\chi^2 = 6.66$, d.f. $= 5$, $P = 0.25$). However, the interaction term in the simpler model was highly significant ($\chi^2 = 24.3$, d.f. $= 1$, $P < 0.001$), indicating that adults had particularly high rates of injury compared with subadults in the mating season, compared with the other two seasons. In 2001, the most parsimonious model contrasted the dispersal season *versus* the other two seasons pooled, with no evidence of an interaction ($\chi^2 = 8.9$, d.f. $= 4$, $P = 0.06$) or any main effect of population class ($\chi^2 = 3.8$, d.f. $= 2$, $P = 0.15$). In 2002,
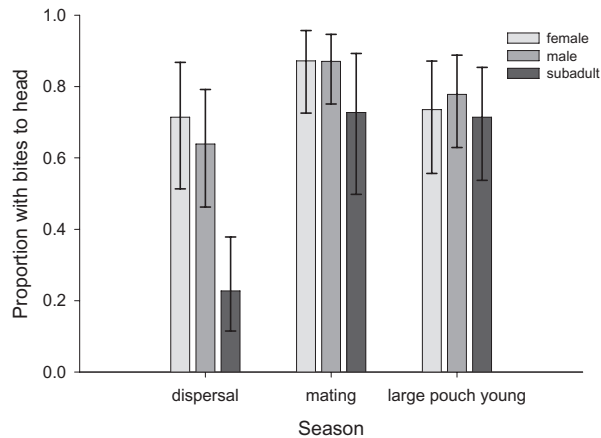
Fig. 6. The proportion of those devils at Freycinet with injuries of severity 2 and above that had bites to the head. The error bars are exact 95% binomial confidence intervals.

the most parsimonious model retained all three seasons and contrasted adults with subadults. The highly significant interaction between age class and season ($\chi^2 = 24.43$, d.f. = 3, $P < 0.001$) was mostly attributable to the high levels of injury to adults compared with subadults in the mating season (Wald statistic = 2.51, $P = 0.01$).

Most injuries on adult males (54.6%) and adult females (65%) were located on the head, and secondarily on the body (adult males 30.6%, adult females 21.6%). Injuries to the tail and limbs were rare in adults. Most injuries recorded on subadults were on the limbs (52.%) and head (25.7%). These summary statistics need to be interpreted with caution, as multiple bites occurred on some individuals. Most injuries resulted in penetration of skin with the most common being simple puncture wound (severity 2) in all population classes (adult males 77.9%, adult females 68% and subadults 86.4%). More severe injury types (severity 3 and 4) such as gouges and bites resulting in the removal of flesh or skin were unusual in all population classes (adult males 11.4%, adult females 6.4% subadults 6.5%). Injuries without tooth penetration (severity 1) were uncommon in adult males (10.6%) and subadults (6.5%) but more common in adult females (25.4%).

Figure 6 shows the proportion of devils with injuries of severity 2 or more that had bites to the head, subdivided by season and population class. Among these injured devils, there was no evidence of differences in injury patterns between years or of interactions including years ($\chi^2 = 12.7$, d.f. = 18, $P = 0.80$), or between males and females ($\chi^2 = 0.6$, d.f. = 3, $P = 0.89$). Adults had a higher proportion of bites to the head in the mating season compared with the other seasons (Wald statistic = 2.92, $P = 0.003$), whereas subadults overall had a smaller proportion of bites to the head than

adults (Wald statistic = 4.34, $P < 0.001$), except when large pouch young were present (Wald statistic = 2.67, $P = 0.0007$).

DISCUSSION

Contact rate and population density

A key result of this study is that contact rates during feeding interactions at carcasses, including both close proximity and biting events, increased with population density. If transmission of tumour cells often occurs during such interactions, we might expect transmission of DFTD to increase with devil population density. However, this study does not directly tell us what proportion of total contacts occurs during feeding interactions compared with other social interactions such as mating or agonistic encounters. Devils contact and injure each other in a variety of social contexts away from food, especially during dominance and mating interactions in the mating season and when newly independent and dispersing juveniles are entering the social dynamic, often in new territory.

For a number of carnivore species, food availability and food dispersion fundamentally influence the structure and spacing of populations (Macdonald 1983; Boutin 1990; Caro 2002; Prange *et al.* 2004) and contact rates (Gilchrist & Otali 2002; Totton *et al*. 2002). As the Tasmanian devil is a specialized scavenger, we might expect the distribution and abundance of carcasses in the landscape to influence foraging contact rates. This warrants further investigation. Devils are exposed to a variety of artificial food sources in Tasmanian landscapes that are regular in time and space and that enhance natural food availability. These include farm carcass dumps, road kill, shot macropod carcasses and open rubbish dumps, all of which can be managed. If predictably occurring or artificially increased food sources were shown to increase contact rates, they would also be likely to increase disease transmission rates, and financial investment in mitigation may be a recommended management action.

A second issue that may influence how contact rate varies with population density is variation in contact behaviour as group size increases. Agonistic behaviour and thus contact rate may intensify with increasing population density as a consequence of more individuals involved in the establishment of social feeding hierarchies and increased resource competition (see Judge & DeWaal 1997).

Who bites whom, where and when?

Interpretation of the injury dataset over 3 years at Freycinet is complicated by the number of high-level

interactions and the differences in the injury patterns observed between the 3 years of the study. There was one consistent pattern, however: we found no indication in any of the 3 years that males and females differed in the proportion of individuals with bite injuries. This is a surprising result, as one might expect that males would have high levels of injury owing to agonistic interactions over access to mates. However, assuming that most disease transmission occurs from biting, this observation is consistent with the lack of any difference in tumour prevalence between the sexes at Freycinet (Lachish *et al*. 2007).

A second key result was in the seasonal patterns of injury between adults and subadults. In 2000 and 2002 injury levels differed between adults and subadults and there were particularly high levels of injury to adults in the breeding season relative to the other two seasons. The seasonal patterns in injury were quite different in 2001, with the highest levels of bites being observed in the dispersal season, just prior to the mating season, and no differences seen between population classes. This may be related to a severe drought in the early part of 2001 (Meteorology Bureau 2001) which included the dispersal season and more than half of the mating season (drought-breaking rain in mid-March 2001). The drought might have led to increased competition among devils of all populations classes over limited food resources. Adult devils were in poor body condition as they were coming into the mating season (M. Jones, unpubl. data 2001) and may have had less energy to invest in competition for mating opportunities. More years of data are clearly required to determine whether 2001 was in fact anomalous, with 2000 and 2002 representing a more 'normal' pattern.

Most of the biting contacts observed during the field behaviour study and most penetrating (severity = 2) injuries recorded at Freycinet occurred on the head. This concurs closely with the location of tumours (Loh *et al*. 2006), as would be expected from an allograft mode of transmission associated with biting (Pearse & Swift 2006). Interactions between devils at carcasses were nearly always face to face, with biting jaws making contact around the mouth and jowls. A penetrating bite would have the potential to inoculate tumour cells into or below the dermal layers. An exception to this pattern was the large number of bites on the limbs of subadults at Freycinet; this result, however, is attributable to just five individuals which had numerous bites on the limbs. The analysis shown in Fig. 6, which treats the individual animal, rather than the bite, as the unit of replication, provides a better description of the location of injuries. A pattern consistent over all 3 years was that, among injured devils, bites to the head were more common in adults than in subadults and head bites to adults were more common in the mating season than in the other two seasons. Taken together, these observations suggest that disease transmission by biting is likely to occur particularly during the mating season.

A fourth important result is that at Freycinet most injuries from bites consisted of single tooth holes of small diameter that penetrated the dermal layer. This would provide ideal conditions for growth of a pathogen or an allograft, provided tissue type was compatible. During our field observations at carcasses it was not possible to estimate whether bites resulted in penetration of the dermal layer.

Implications for disease management and conservation

An apparent inconsistency between the two datasets is the overall lower injury rate of subadults in the Freycinet data, in contrast to the high proportion of total bites that were delivered from subadults at three different sites (Bronte Park, Narawntapu and Woolnorth) and received by subadutls at one particular site (Woolnorth) in the directly observed interactions around carcasses. Whilst temporal or spatial variation in behaviour cannot be ruled out as an explanation at this point, a possible cause for this inconsistency is that most injuries from biting do not occur during feeding interactions. Bites delivered during feeding interactions may not be so hard as to penetrate the dermis. They therefore may not be detectable as 'injuries' in trapped animals. Such non-penetrating bites would be less likely to lead to disease transmission than penetrating injuries. The high rate of injury to adults relative to subadults during the mating season in two of the three years of the Freycinet data suggests that much of the total penetrating biting may occur during mating encounters. This is consistent with the expectation that the stakes and costs of the outcome of mating encounters is higher than those of feeding interactions.

Determining the role of transmission during mating, relative to transmission during feeding encounters, is critical for understanding the ecology of the disease and potential development of control strategies. Our data show that biting contacts during feeding encounters are dependent on devil density. If this is the dominant mode of contact, it would suggest that the disease alone is not capable of driving the devil to extinction and means that density manipulation may be an effective control strategy (Bradshaw *et al*. 2006; McCallum & Jones 2006). In contrast, if most penetrating biting contacts occur during mating behaviour, then DFTD is likely to have many of the characteristics of a sexually transmitted disease, including frequency dependence and the ability to drive the host to extinction or to a very low population density. Density manipulation would be counter-productive in this case, although

selective removal of infected animals, particularly those that make multiple contacts, might be an effective strategy (McCallum & Jones 2006; Jones *et al.* 2007). Our results from two of the three years at Freycinet do suggest that a peak of biting contact to adults resulting in injuries (and thus probably disease transmission) is associated with the mating season, with the implication that these injuries have occurred during mating encounters. However, the contrasting result from the drought year of 2001 means that we must be cautious in drawing firm conclusions. A further indication of the limited role of density dependence in disease transmission is the spread of the disease well into naturally very-low-density parts of the devil's range (Hawkins *et al.* 2006; McCallum *et al.* 2007)

If the peak of biting contact resulting in injuries, and thus probably disease transmission, is associated with the mating season, intensifying disease control in the months prior to the mating season could be an effective strategy to reduce transmission and thus R_0. Identification of potential 'superspreader' age and sex classes or likely individuals might also increase effectivity of disease control. This study suggests that breeding adult males and females engage in more biting behaviour likely to transmit disease than subadults. In addition, disease is at lower prevalence in subadults than adults (Lachish *et al.* 2007). Most disease transmission is thus likely to occur from adults. However, both datasets had limitations. The field behavioural data were based only on feeding interactions and the injury data were temporally variable and did not provide direct information on behaviour in the field. A more detailed study with a contact population network approach is needed, both to further investigate the relative importance of mating interactions, agonistic interactions and feeding interactions in biting behaviour and to identify potential superspreader individuals or demographic classes.

ACKNOWLEDGEMENTS

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