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Contact rates between possums revealed by proximity data loggers

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Summary

1. Information on close interactions between wild animals is difficult to obtain for cryptic species, but is important for understanding their social and mating systems as well as the dynamics of directly transmitted diseases.
2. The persistence of bovine tuberculosis (Tb) in New Zealand is enhanced by the presence of wildlife hosts for the infection, principally the brushtail possum *Trichosurus vulpecula*. Quantifying the relationship between the frequency of contacts and possum population density is important for understanding the dynamics of the disease and the potential effectiveness of different methods for disease control.
3. We used novel proximity data loggers to record contacts (< 40 cm distance) between individual male and female wild-living brushtail possums over 3 years at three different sites with a range of habitats and population densities.
4. Most contacts between male and female possums appeared to be sexual in nature, and contact rate was not related linearly to population density. Contacts occurred more frequently during the breeding season, when a female possum could interact with up to four males. However, even during this peak contact period the average contact rate was equivalent to only one contact every 2 days.
5. The total duration of contacts was significantly higher during the breeding season. During this time, contacts lasting for more than 1 min occurred episodically. A small proportion (2·3%) of the interactions lasted for 5–15 min, although the mean duration of contacts was only 18–26 s 24 h^{-1}. Outside the breeding season, contacts were brief and infrequent.
6. The frequency of contacts showed a slight increase when the possum density increased sharply at the main study site, although the duration of contacts was unaffected. This increase in contact rate may have been the result of an influx of new animals causing perturbation to the existing population.
7. Previous paternity analysis using DNA profiling indicated that the possum mating system is polygynous, with males being promiscuous. Our data reveal that females are probably also promiscuous and that the mating system of possums may therefore be polygamous, including both polygyny and polyandry.
8. *Synthesis and applications.* Most contacts between possums occur in the peak mating season and appear to be related to mating and associated behaviour. There are some contacts outside the main mating season, but these are infrequent. The transmission of bovine Tb infection in possum populations may therefore occur by other routes in addition to direct contact. The non-linear (frequency-dependent) contact rate–density relationship recorded provides some insight as to why repeated population reduction is necessary to achieve lasting Tb control in possum populations. It also provides some support for the role that could be played by sexually transmitted, viral-vectored immunocontraception in the control of possum populations, either alone or in conjunction with more traditional control methods.

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Introduction

Information on interactions between wild animals is important for understanding social behaviour, mating systems and the prevalence and spread of parasites and disease. Some diseases of wildlife may also pose a threat to humans and/or livestock. For example, foxes *Vulpes vulpes* L. in the UK act as a reservoir for rabies (White, Harris & Smith 1995), and badgers *Meles meles* L. in the UK (Gallagher & Clifton-Hadley 2000) and brushtail possums *Trichosurus vulpecula* Kerr in New Zealand (Coleman *et al*. 1994; Jackson *et al*. 1995; Caley *et al*. 1999; Coleman & Caley 2000) act as reservoirs for bovine tuberculosis (Tb). The potential opportunities for the spread and maintenance of infection of a contact-transmitted disease within a wildlife host population depend on patterns of contact between individual animals.

The idealized relationship between transmission and population density may take one of two forms. For some diseases, the contact rate increases as host population density increases, and the transmission rate also increases with the density of infectious individuals (density-dependent transmission; Begon *et al*. 2002). However, for other diseases, such as those reliant on sexual transmission or those occurring in socially structured host populations, the contact rate may remain constant over a large range of densities, and transmission is dependent on the prevalence of infection (frequency of infectious individuals) rather than population density (frequency-dependent transmission; Begon *et al*. 2002). In practice, transmission is unlikely to conform to either of these idealized transmission–density relationships (De Jong, Diekmann & Heesterbeek 1995; Begon *et al*. 1998; Caley *et al*. 1998; McCallum, Barlow & Hone 2001; Ramsey *et al*. 2002). Moreover, neither model relationship accounts for the effects of spatial heterogeneity on the distribution and abundance of hosts and infectious agents. For some infections, particularly those in patchily distributed hosts, global persistence is a product of complex interactions across the landscape, involving heterogeneities in host behaviour, dispersal, habitat and landscape structure (Foley, Foley & Pedersen 1999; Keeling & Gilligan 2000; Caley, Coleman & Hickling 2001; Smith 2001). In some cases, potential contact rates (White & Harris 1995; Barlow 1996; Tuyttens *et al*. 2000) or actual disease transmission (Caley & Ramsey 2001) may also be affected by management-induced perturbations. Thus it is likely that population density, social structure, habitat and disturbance all contribute to determining contact rates and transmission–density relationships.

Interactions between individuals are difficult to measure in the wild, particularly for nocturnal and cryptic species, and so data on interactions, and in particular their relationships with population density and habitat, have been limited by the available technology. The best attempts to measure contact rates in wildlife populations have been based on simultaneous radio-tracking data, where 'contacts' are assumed to reflect patterns of close encounters within a specified distance, chosen to reflect the resolution of the radio-tracking data rather than having any biological basis (White & Harris 1994; White, Harris & Smith 1995; Ramsey *et al*. 2002; Dexter 2003). The relationship between close interactions, actual contact behaviour and disease transmission is unknown, but transmission is difficult to measure directly for many infections. Moreover, specific hosts may be affected by a number of diseases of ecological or economic significance, or may be considered as possible candidates for viral-vectored immunocontraception, in which case disease-specific estimates of transmission may be of limited value. A knowledge of the mechanisms underlying transmission, such as behavioural interactions and contact rates, provides a much broader base of understanding for the management of many types of infectious agents in host populations.

Brushtail possums are nocturnal, arboreal marsupials that were introduced to New Zealand from Australia in the 1840s to establish a fur industry. They later became major environmental and agricultural pests (Pracy 1962; Clout & Ericksen 2000). Possums damage biodiversity by selective browsing in indigenous forests (Meads 1976; Batcheler 1983; Payton 2000) and by preying on native invertebrates (Cowan & Moeed 1987) and the eggs and nestlings of native birds (MacLennan 1984; Brown, Innes & Shorten 1993). They are also considered to be the primary wildlife reservoir of Tb in New Zealand (Coleman 1988; Coleman & Caley 2000). Despite all control efforts, their distribution on the mainland of New Zealand has expanded in the past 15 years to include most of the country (Clout & Ericksen 2000). In many habitats, possums occur at densities up to 20 times those in their native Australia (Cowan 1990). Biological control, especially immunocontraception, has been investigated as a control method (Cowan 2000).

Contacts during mating are thought to be the major route of Tb transmission within possum populations (Morris & Pfeiffer 1995). Quantifying contact behaviour in possum populations, particularly during breeding periods, is therefore important for modelling disease transmission. It is also important for predicting the effectiveness of biological control that depends on interactions between individuals. Recent studies using minisatellite DNA profiling and microsatellite profiling have revealed that male possums are promiscuous. The possum mating system is polygynous, with a high proportion of males siring no offspring and some siring up to four young in a breeding season (Sarre *et al*. 2000; Taylor *et al*. 2000; Ji *et al*. 2001). However, DNA techniques based on paternity analysis can only detect successful matings; they cannot detect unsuccessful matings or non-sexual interactions. Because a female possum usually produces only one young during a breeding season (Pilton & Sharman 1962), the number of males a female may mate with during a breeding season cannot be detected by DNA methods. The conclusion of a polygynous mating system of possums, based solely on paternity analysis using DNA techniques, is therefore incomplete. Molecular methods also cannot detect non-sexual interactions such as fighting. While the brushtail possum is a well-studied species and the subject of more than 2000 publications (Clout & Sarre 1997), the patterns of interactions in this nocturnal, arboreal and solitary species are difficult to observe and are still largely unknown.

In this study, we used data from novel proximity data loggers, previously tested on captive possums (Ji *et al*. 1999), to measure the frequency and duration of contacts between wild-living individual male and female possums during the breeding season at three sites with contrasting habitat types and population densities. We use these data to derive estimates of contact rates between male and female possums, and to examine the relationships of contact rate with population density and habitat.

Methods

PROXIMITY DATA LOGGERS

We used proximity data loggers (patent NZ506431) fitted to individual possums to record the close proximity of any other individual possum fitted with a pulse-controlled transmitter (Ji *et al*. 1999). Transmitters used in this trial (made by Sirtrack Ltd, Havelock North, New Zealand) transmitted on the 160-MHz waveband. Each transmitter had a unique pulse rate, between 0·8 and 1·5 s^{-1}, thereby allowing identification of individual possums. Each data logger weighed about 30 g and was fitted on a collar around a possum's neck in the same way as a radio-transmitter. The detection distance of the data loggers was 40 cm. If a transmitter was within recording range, the time, date and duration of its presence were recorded and stored by the data logger. The data were then downloaded to a computer for analysis.

STUDY SITES

The main study site was at Coatesville reserve (36°44′S, 174°40′E), about 20 km north of Auckland, New Zealand. The vegetation at this site consists of mixed broadleaf podocarp forest fragments surrounded by pasture, orchards, pine plantations and gardens associated with housing. The original possum population was eradicated in 1997 and has since recovered. The present study commenced in 1999, 2 years after the eradication programme, and continued for 3 years. We also used two other sites, at Huapai (36°47′S 174°45′E), north-west of Auckland, and Mangatawhiri (37°14′20″S, 175°02′E), south of Auckland. The vegetation at Huapai is mixed broadleaf podocarp forest surrounded by pasture and gardens associated with housing. The vegetation at Mangatawhiri mainly consists of introduced willow (*Salix* spp.). The population densities of possums at Coatesville and Huapai were estimated based on capture–mark–recapture data from each trapping session using the Jolly–Seber method. The population density at Mangatawhiri, also based on Jolly–Seber estimates from capture–mark–recapture data, was 8–9 possums ha^{-1} (Poutu 2000), taken as a mean density of 8·5 possums ha^{-1} for our analysis.

DETECTION OF CONTACTS IN THE FIELD

A contact was defined as two possums being in very close proximity, as recorded by a data logger. Such close interactions include physical contacts, for example mating, mounting, allogrooming and fighting.

At Coatesville and Huapai, the majority of possums breed in autumn (March–May); only a very small proportion breeds in spring (September–November) (Ji, Clout & Sarre 2000). Our fieldwork included the autumn breeding season (early March to late April). Fieldwork consisted of two trapping sessions each year, from mid-January to mid-February to fit data loggers and transmitters on possums, and from mid-May to mid-June to recover the data loggers for downloading of data. At Mangatawhiri, 47% of females breed during spring (Poutu 2000), with a birth peak in October. At this site, our initial trapping session was in early September and our second trapping session, to retrieve the loggers and transmitters, was in November. At all three sites we set out possum cage traps at intervals of 50 m, in a trapping grid comprising an area of 3·75 ha at Coatesville and Huapai, and 3 ha at Mangatawhiri. During each trapping session, the traps were operated for three nights per week over 4 weeks. We baited the traps with apples dusted with fruit-flavoured flour. On its first capture, a possum was anaesthetized with gaseous ether and then tagged with two uniquely numbered ear tags. Sex, maturity, weight and body measurements (total length, tail length and width of testes) were recorded on the first capture in each trapping period. During the pre-breeding trapping session, we fitted each adult female (with a developed pouch) with a data logger. Males with a testis width greater than 15 mm were regarded as mature (Ji, Clout & Sarre 2000) and each mature male was fitted with a radio-transmitter with a unique frequency and pulse rate. Most (> 90%) local adult males were radio-tagged. During the post-breeding trapping session, we removed all data loggers recovered from possums for data downloading. All procedures performed were within animal ethics guidelines (The University of Auckland, Auckland, New Zealand, approval number N970).

Estimation of contact rates

We converted the contact data from individual female possums to 24-h contact rates by dividing the total number of contacts by the number of days for which each logger was attached to a possum. As we had fitted transmitters to a high proportion of all the males present within our study areas, and there was no relationship between the number of males contacted and the number of males present (see the Results), these data were taken to be equivalent to 'total' contact rate figures.

Variation in contact rates

We examined the temporal and spatial variation in contact rates by combining the measurements from the three sites. The number and duration of contacts per 24 h were $\log_{10}$-transformed prior to the analysis to reduce non-normality in the data (Zar 1999). We used repeated-measures analysis of variance (ANOVA) to compare the number and duration of contacts per 24-h period across the sites, and used restricted maximum likelihood (REML) within the SAS statistical package (SAS Institute, Cary, NC) to estimate the coefficients related to the independent factors of year and month (site was initially considered as an independent factor, but had zero degrees of freedom when included in the model with year and month so was excluded from the final analysis). In the analysis, individual possums were the subjects, year × month was the repeated effect and a first-order autoregressive covariance structure was used because of potential time-dependence in the data between successive time periods. The significance levels of the independent factors were assessed using the Satterthwaite t-test for unequal variances.

Results

Population densities

The Jolly–Seber estimates of population density (possums ha^{-1}) at Coatesville varied from 3·3 (95% confidence limits 2·9 and 5·6) in May–June 1999 to 5·9 (95% confidence limits 4·4 and 11·1) in January–February 1999 (Table 1). The population density at Huapai in January–February 1999 was estimated as 4·1 possums ha^{-1} (Table 1). No confidence limits could be calculated from this session's data for Huapai because of a poisoning control operation in the subsequent session. The large confidence intervals around the population estimates from Coatesville precluded their use as reliable measures of variation in density at the site.

Data recorded by loggers

Twenty-two of 33 loggers recovered from 17 females (including three at Coatesville and one at Huapai that were present in two breeding seasons) recorded data (Table 2). Of these, four loggers at Coatesville worked

Table 1. Jolly–Seber estimates of population density at Coatesville and Huapai for each trapping session. No confidence limits could be calculated for January–February 1999 at Huapai because of a poisoning operation in the subsequent season

Site	Time period	Population density (possums ha^{-1})	Lower 95% confidence limit	Upper 95% confidence limit
Coatesville	Jan–Feb 1999	5·9	4·4	11·1
	May–Jun 1999	3·3	2·9	5·6
	Jan–Feb 2000	3·5	2·8	7·0
	May–Jun 2000	4·0	2·9	8·5
	Jan–Feb 2001	4·2	3·3	8·3
	May–Jun 2001	4·9	3·6	11·3
Huapai	Jan–Feb 1999	4·1	–	–

Table 2. Number of brushtail possums fitted with data loggers at Coatesville, Huapai and Mangatawhiri during 1999–2001

	Coatesville			Huapai			Mangatawhiri		
Year	Loggers used	Loggers recovered	Loggers with data	Loggers used	Loggers recovered	Loggers with data	Loggers used	Loggers recovered	Loggers with data
1999	7	4	2	8	6	3	9	7	4
2000	7	7	6	7	1	1			
2001	9	8	6						
Total	23	19	14	15	7	4	9	7	4

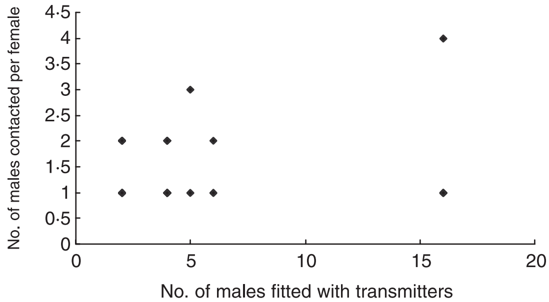

Fig. 1. The relationship between the number of male brushtail possums interacted with by females and the number of males fitted with transmitters.

throughout the entire period for which they were attached to females. The others stopped working before they were removed from the animal, because of battery failure or damage by the animals. Data obtained from these latter loggers varied regarding the length of time over which interactions were recorded. One logger at Mangatawhiri recorded co-denning between the female and a male fitted with a transmitter. The memory of the logger was filled up during 1 day. The data from this logger were excluded from the analysis.

All 22 females carrying loggers made contact with at least one male during the period when data were collected; 14 females interacted with two or more males (Table 3). There was no evidence that a higher number of radio-tagged males present at the study sites led to an increase in the number of males with which a female interacted (Fig. 1; $r_s = 0{\cdot}005$, d.f. = 44, NS).

DISTRIBUTION OF CONTACTS DURING THE BREEDING SEASON

At Coatesville, one data logger in 1999, two in 2000 and one in 2001 worked throughout the autumn breeding season. The numbers of interactions with radio-tagged males, recorded by the data loggers of these four females during the breeding season, were 8, 10, 11 and 48, respectively. All interactions were recorded between mid-February and early May. Interactions happened episodically, with long intervals between them (Fig. 2).

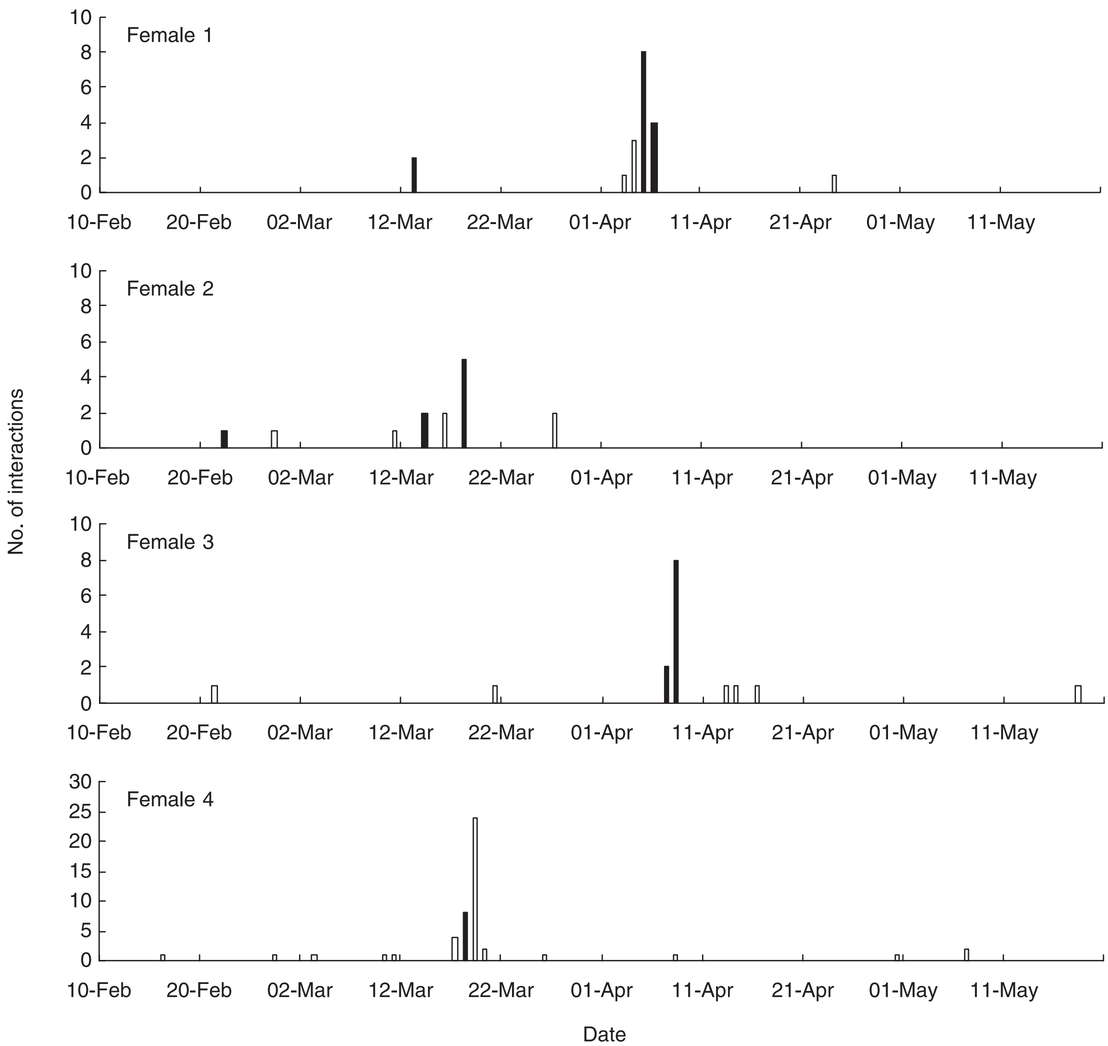

Fig. 2. Interactions of four female brushtail possums with radio-tagged males during the mating season at Coatesville, New Zealand (open bars, interactions lasting up to 1 min; closed bars, interactions lasting more than 1 min).

Table 3. Minimum number of male brushtail possums contacted by females

Year	Site	No. males with transmitters	No. females in contact with males			
			1 male	2 males	3 males	4 males
1999	Coatesville	4		2		
	Huapai	6	2	1		
	Mangatawhiri	16	2	1		1
2000	Coatesville	4	1	2	2	1
	Huapai	5			1	
2001	Coatesville	2	2	2	2	

Table 4. Parameter estimates and *t*-statistics from comparisons of differences of least-squares means relating to the number and duration of contacts per 24-h period (log-transformed). Only differences with *t*-statistics significant at $P < 0{\cdot}10$ are shown

	Effect	Comparison	Estimate ± SE	d.f.	*t*	*P*
No. of contacts per 24 h	Month	Apr–Feb	0·13 ± 0·05	18·5	2·45	0·02
		Apr–May	0·14 ± 0·07	20·9	1·92	0·07
Duration of contacts per 24 h (s)	Month	Mar–Feb	0·58 ± 0·21	19·5	2·75	0·01
		Mar–May	0·69 ± 0·30	17·1	2·31	0·03
		Apr–Feb	0·76 ± 0·24	19·1	3·11	< 0·01
		Apr–May	0·86 ± 0·33	20·9	2·62	0·02
		Oct–Sep	0·90 ± 0·38	17·2	2·35	0·03

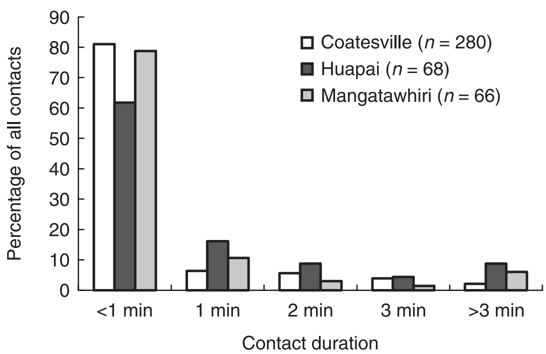

Fig. 3. Duration of interactions between female and male brushtail possums.

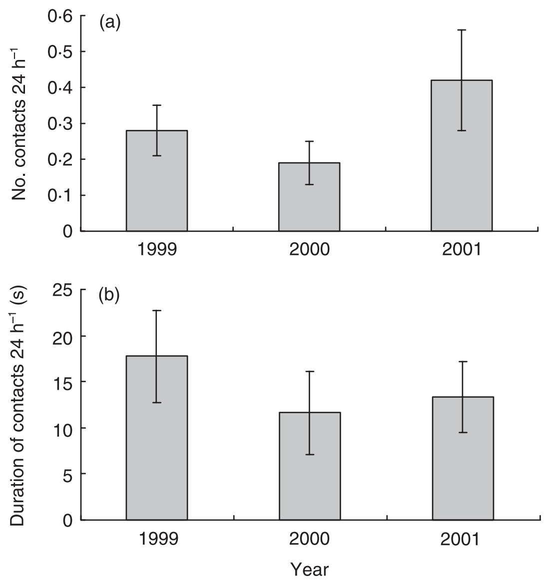

Fig. 4. Mean (± SE) (a) number and (b) duration of contacts with male possums per female in the different years. Loggers and transmitters were fitted to possums at Coatesville in 1999, 2000 and 2001, Huapai in 1999 and 2000, and Mangatawhiri in 1999.

No interaction lasting more than 1 min was recorded after mid-April for any of these females.

TOTAL DURATION AND RATES OF CONTACTS

In total 414 interactions between females and males were recorded at the three study sites from all data loggers that were operational for varied time periods. Most interactions (60% at Huapai, 78·8% at Mangatawhiri and 80% at Coatesville) were brief, lasting up to 1 min. Only 20–40% of interactions were more than 1 min long (Fig. 3).

The number of contacts with males per female per 24 h (contact rate) was greater in 2001 than 2000 and 1999 (Fig. 4). The contact rate was also greater in March and April at Coatesville and Huapai, and in October at Mangatawhiri (Fig. 5), although even during these peak times the mean was only 0·39–0·55 contacts 24 h^{-1} (one contact every 2 days). Neither the yearly nor monthly differences were significant overall ($F_{\text{year } 2,8{\cdot}9} = 1{\cdot}25$, $P = 0{\cdot}33$; $F_{\text{month } 5,17{\cdot}2} = 1{\cdot}91$, $P = 0{\cdot}14$), although comparison of the differences of least-squares means indicated that the number of contacts in April was significantly greater than that in either February or May (Table 4). There was no clear relationship between the mean number of contacts per month during the peak breeding periods and population density across the different sites (Fig. 6).

The total duration of contacts with males per female was significantly affected by month ($F_{\text{month } 5,17{\cdot}8} = 4{\cdot}15$,

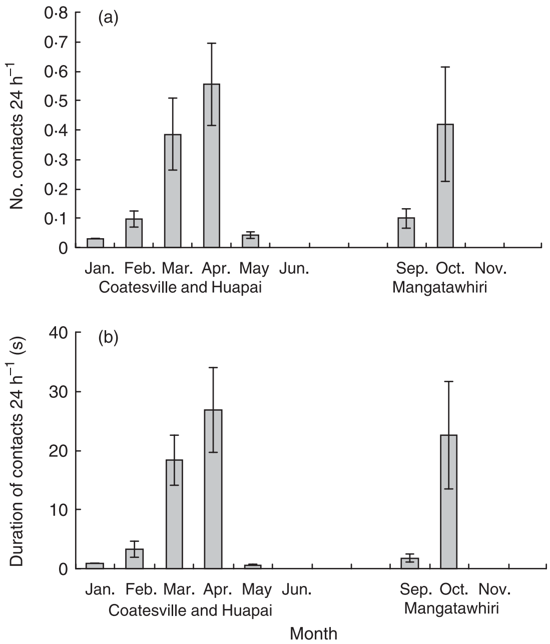

Fig. 5. Mean (± SE) (a) number and (b) duration of contacts with male possums per female in the different months. Loggers and transmitters were fitted to possums between January and May at Coatesville and Huapai, and September and October at Mangatawhiri.

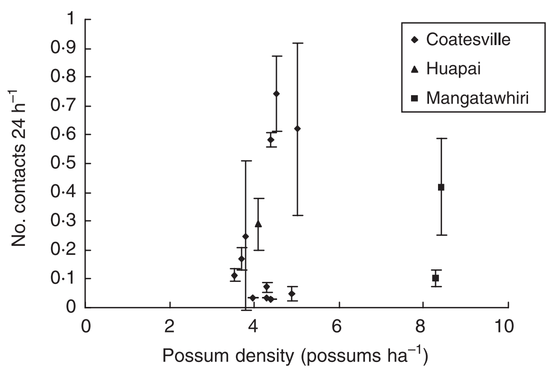

Fig. 6. Relationship between mean monthly male–female contact rate during the peak breeding periods (March and April 1999, 2000 and 2001 at Coatesville, March 1999 at Huapai, October 1999 at Mangatawhiri) and population density. Population densities at Coatesville and Huapai were taken as the means of the January–February and May–June Jolly–Seber estimates. Data relating to the same population density estimates are offset on the *x*-axis by 0·1 possums per hectare for clarity.

$P = 0{\cdot}01$). Contacts were of longest duration in March and April at Coatesville and Huapai, and in October at Huapai (Fig. 5 and Table 4). However, even during these peak periods the mean duration of contacts was only 18–26 s 24 h^{-1}. There was no significant difference in the duration of contacts between years (Fig. 4).

Discussion

The early failure of some data loggers meant that records of contacts for certain individual possums were not complete over the period for which they were fitted. However, assuming these were random failures, and because we standardized the number and duration of contacts per 24-h period for the analysis, this should not bias our analysis in any way.

Our data have revealed some important aspects of possum interactions. Most contacts between male and female possums appeared to be sexual and were largely independent of population density. However, even during the peak breeding season contacts were infrequent and the average contact rate between female and male possums was equivalent to one contact every 2 days. Most contacts between female and male possums were short, lasting up to 1 min. These interactions could be either agonistic in nature or males trying to mount females that were not receptive between oestrous cycles. Only 22% of 414 interactions recorded during the breeding season lasted for more than 1 min. These interactions were more likely to involve mating, which in possums typically lasts for 2–4 min (Winter 1976). A small proportion (2·3%) of the interactions recorded lasted for 5–15 min. Interactions lasting more than 5 min may involve allogrooming between females and males. This has been observed between consorting females and males, individuals sharing a den and mothers and young (Winter 1976; Day *et al*. 2000).

We found no difference in the frequency or duration of contacts between the sites, despite the fact that the average possum density at Mangatawhiri was approximately twice that at Coatesville and Huapai. This non-linear contact rate–density relationship is more representative of frequency-dependent than density-dependent transmission, reflecting the fact that the male–female contacts that we recorded were principally concerned with mating and/or allogrooming, a behaviour that is likely to occur between consorting animals before and after mating (Winter 1976). Such sexually related contacts are less likely to show simple linear density-dependence than non-sexual ones (Barlow 1994; McCallum, Barlow & Hone 2001). Indeed, based on radio-tracking data, Ramsey *et al*. (2002) demonstrated a non-linear convex-up relationship between the number of close (< 10 m) male–female interactions and male population density in an experimentally reduced possum population. Our contact rate data (Fig. 6) also conformed to a non-linear convex-up relationship. In contrast, Caley *et al*. (1998) reported that den-sharing among possums showed a non-linear convex-down relationship with possum density. However, although male–female dyads did share dens in their study, most den sharing they recorded was between female–female dyads. This further suggests that the interactions we recorded in this study were primarily concerned with mating or allogrooming activity.

The frequency of close interactions was greatest in 2001, when the only site monitored was Coatesville. The population at this site was recovering following a depopulation event in 1997. Initial population recovery was mostly the result of range shifts by neighbouring

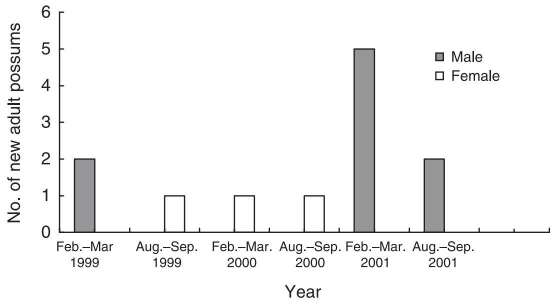

Fig. 7. Number of new adult possums recorded at Coatesville between February–March 1999 and August–September 2001.

animals (Ji *et al*. 2004). After the initial influx, a small number of new possums was recorded each year, and more than twice as many new adult males were recorded during 2001 (Fig. 7). The resulting perturbation to the existing population may have been responsible for the increase in contacts in 2001, as has been hypothesized in relation to culling badgers to control bovine Tb in the UK (Tuyttens *et al*. 2000). The fact that there was no corresponding increase in the mean duration of contacts suggests that the frequency of longer-duration contacts, such as mating and allogrooming, remained relatively unaffected by this perturbation.

In all years, interactions were of longest duration during the peak of the breeding season (March–April at Coatesville and Huapai, and October at Mangatawhiri). At Coatesville and Huapai, the loggers were fitted on possums from late January to early June, but few interactions were recorded before mid-February or after early May, and all interactions lasting more than 1 min recorded by the loggers that worked throughout the breeding season at Coatesville were between late February and late April. Of the four females for which complete data were collected for the breeding season, two had only one bout of long contacts (more than 1 min), during which mating may have occurred. The other two females had two bouts of long contacts. The intervals between these long contacts were 19 and 20 days for these two females, respectively. These intervals were slightly shorter than the oestrous cycle of female possums reported for captive possums, which varied from 21 to 32 days (Lyne 1959; Pilton & Sharman 1962; Rekha 1997).

Agonistic interactions between possums range in form and intensity from 'give-way' to 'threats' and 'fights' (Jolly 1976; Winter 1976; Biggins & Overstreet 1978; Day *et al*. 2000). Threats are the most frequently observed type of interaction (Day, O'Connor & Matthews 1998). High-intensity interactions such as fighting tend to occur between possums with similar dominance status (Winter 1976), with females dominant over males (Winter 1976; Jolly & Spurr 1996). A relative lack of contacts between female and male possums outside the peak breeding season is consistent with the assumption that spacing between males and females in the non-breeding season is maintained by scent marking and low-intensity behaviour that does not result in physical contact (Winter 1976; Day, O'Connor & Matthews 1998; Day *et al*. 2000) and the observations that non-sexual interactions between wild individuals are rare (Jolly 1976; Winter 1976; MacLennan 1984; Herbert & Lewis 1999).

Paternity analysis using DNA profiling indicates that the possum mating system is polygynous, with males being promiscuous (Sarre *et al*. 2000; Taylor *et al*. 2000; Ji *et al*. 2001). Our data reveal that females are probably also promiscuous. During one breeding season, a female possum could have close interactions with up to four males. Most of the females had interactions, lasting for more than 1 min, with at least two males during each breeding season. Our preliminary data suggest that female possums are promiscuous and that the mating system of possums may therefore be polygamous, including both polygyny and polyandry. However, data loggers cannot distinguish between close proximity, contacts and mating; further study is needed to confirm female promiscuity in possums.

Disease transmission in populations with polygamous mating system will be faster than in a monogamous or polygynous-only mating system. A polygamous mating system will also favour biological control methods that depend on close interactions such as sexual contacts to spread the control agents. The brushtail possum is a species that is not only opportunistic in its feeding habits (Green 1984; Cowan 1990; Nugent *et al*. 2000) but also in its breeding behaviour. The breeding patterns of brushtail possums vary between populations. Patterns include synchronous breeding in autumn (Tyndale-Biscoe 1955; Lyne & Verhagen 1957; Smith, Brown & Frith 1969; Hocking 1981); a main birth peak in autumn and a smaller peak in spring (Tyndale-Biscoe 1955; Smith, Brown & Frith 1969); a main birth peak in autumn but births in most months of the year (Dunnet 1964; Gilmore 1969; Smith, Brown & Frith 1969; Clout 1977); and non-synchronous breeding without a major birth peak (Pilton & Sharman 1962; Kerle 1983). Such variation in breeding seasonality may lead to variation in the degree of promiscuity (Emlen & Oring 1977; Say, Pontier & Natoli 2001), thereby leading to variation in patterns of interactions between male and female possums.

Our data suggest that most contacts of long duration between possums are connected with mating behaviour. There is an additional background level of contacts occurring outside as well as within the main mating season, although our data cannot reveal anything about the likely nature of these contacts. However, these contacts are clearly infrequent, which suggests that routes other than direct contact may be significant in the transmission of infection. Without supporting data on actual transmission rates, it is not possible to quantify precisely the relative importance of longer and shorter contacts in the transmission of Tb in possum populations. Nevertheless, the frequency-dependent pattern of the contacts we recorded provides some evidence as to why repeated control is necessary to achieve lasting

Tb reductions in possum populations in the field (because of the non-linear contact rate–density relationship). It also provides support for the important role that could be played by a sexually transmitted, viral-vectored immunocontraception in the control of possum populations (Barlow 1994), either alone or in conjunction with more traditional control methods. Understanding the relative roles of habitat and landscape structure, population density, culling-induced perturbation and the potential disruptive influence of immunocontraception (Caley & Ramsey 2001) on contact patterns in possum populations, and particularly the role of different types of contact in disease transmission, will enhance the scientific basis for successful management of bovine Tb in possums, both now and in the future.

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