ORIGINAL PAPER

Spatial and temporal heterogeneities in the contact behaviour of rabbits

**Maija K. Marsh · Michael R. Hutchings ·
Steven R. McLeod · Piran C. L. White**

Abstract It is becoming increasingly evident that the social behaviour of many group-living species is more complex than previously assumed and that free mixing of individuals, even within social groups, is rare. This has important implications for ecological processes, such as disease transmission, which are dependent on interactions between individuals. European wild rabbits (*Oryctolagus cuniculus*) have been considered traditionally as highly sociable animals that mix freely within groups but interact less frequently between groups. We deployed proximity logging devices to quantify the intra- and inter-group contact behaviour of free-living wild rabbits in two populations in a temperate region of Australia. Altogether, 126 rabbits were fitted with proximity loggers at least once during the study. Radio-tracking was carried out alongside proximity data collection to determine the space use of rabbit social groups within the study sites. On average, a rabbit made only 1.54±0.23 (SE) (median=0.54) contacts per day with each other rabbit carrying a proximity logger in its social group, and the mean daily contact duration was 202±38 s/day (SE) (median=29 s). Despite the high degree of home range overlap between the neighbouring social groups, inter-group contacts were highly infrequent and brief. Our results demonstrated considerable spatial and temporal heterogeneities in the contact behaviour between individual rabbits, both between populations and between and within social groups in the same population. Such variations in the social organisation of rabbits are likely to create complex patterns of disease transmission through direct contact and may contribute towards observed heterogeneities in the effects of disease on wild rabbit populations.

Keywords Australia · Heterogeneity · Home range · Rabbit haemorrhagic disease virus · Social interaction · Social organisation · Wildlife disease

M. K. Marsh · P. C. L. White (✉)
Environment Department, University of York,
York YO10 5DD, UK
e-mail: pclw1@york.ac.uk

M. R. Hutchings
Disease Systems, Scottish Agricultural College,
West Mains Road,
Edinburgh EH9 3JG, UK

S. R. McLeod
Vertebrate Pest Research Unit,
New South Wales Department of Primary Industries,
Forest Road,
Orange, NSW 2800, Australia

Introduction

Social organisation of group-living vertebrates may vary in relation to extrinsic (environmental) and intrinsic (population-related) factors such as resource availability, habitat quality, season, climate, density and age structure. The pattern of social interactions in these species is therefore likely to show some variability between different populations. Numerous studies have shown that different individuals fulfil different roles in a social hierarchy. For example, dominant individuals can play a more important role in territorial defence than subdominants and males more than females (Schradin 2004; Le Roux et al. 2008; Rosell et al. 2008). However, it is also increasingly recognised that there may be considerable variation in behaviour between

individuals, which extends beyond social group structures or hierarchical roles (Böhm et al. 2009). Such heterogeneities in individual social behaviour can have a considerable impact on population ecology and survival, including gene and information flow, resource utilisation and the spread of infectious pathogens that transmit through direct contact between individuals (Andreasen and Christiansen 1989; McCallum et al. 2001; Newman 2002; Meyers et al. 2005; Whitehead 2009). However, the contact patterns of many free-ranging wild vertebrate populations are still poorly quantified.

Epidemiological models on the direct transmission of pathogens often assume homogeneous mixing of individuals, either across the whole population or within its constituent social groups. Social organisation has also been shown to vary temporally in relation to changes in activity connected with breeding and dispersal (White and Harris 1994; Ji et al. 2005; Böhm et al. 2008). Even though epidemics can be highly sensitive to such patterns of mixing (Lloyd-Smith et al. 2005), spatial and temporal heterogeneities in a social organisation are rarely included in host–disease models. This is because data on contact rates in wild populations are scarce, largely because they are difficult to measure in the field. Advances in the measurement of direct interactions among free-living animals have become possible recently through the use of proximity loggers. Unlike traditional methods such as direct observation (Cowan 1987a, b; Mitani et al. 2002; Mollema et al. 2006), recording co-occurrence of individuals during sightings or censuses (Vonhof et al. 2004; Lusseau et al. 2006), and radio-telemetry (White and Harris 1994; White et al. 1995, 2003; Böhm et al. 2008), proximity loggers provide continuous and unbiased high-resolution data on the close contacts between free-ranging animals (Ji et al. 2005; Prange et al. 2006; Böhm et al. 2009).

Here we use proximity loggers to investigate the social contact behaviour of European wild rabbits (*Oryctolagus cuniculus*) in two sites with apparent differences in habitat quality in a temperate region of Australia. Unlike in Southern Europe where the rabbit is a keystone species which provides an important food source for several endangered predator species (Delibes-Mateos et al. 2007, 2008; Moreno et al. 2007), rabbits have become one of the most damaging vertebrate pests in Australia since their arrival in 1859 due to their devastating impacts on agriculture and biodiversity (Williams et al. 1995; Edwards et al. 2004; McLeod 2004). Since the introduction of myxomatosis in the 1950s, biological control using disease has formed a mainstay of Australian rabbit population control. In response to the declining effectiveness of myxomatosis, a second disease agent, rabbit haemorrhagic disease virus (RHDV), was introduced to Australia in the 1990s to aid the existing rabbit control (Cooke and Fenner 2002). RHDV, which presents a conservation problem in Southern Europe due to its severe impacts on the native rabbit populations (Moreno et al. 2007), was at first highly effective in reducing rabbit numbers also in Australia (Mutze et al. 1998). However, since the promising initial reports, the effectiveness of the virus has been inconsistent and mathematical simulations of the rabbit–RHDV system based on homogeneous mixing (Barlow and Kean 1998; Barlow et al. 2002) have failed to explain the variability in RHDV spread and persistence at different locations.

As one of the main routes of RHDV spread is through oral and nasal transmission during direct contact (Cooke and Fenner 2002), social organisation of rabbits may be an important factor contributing towards the observed variations in RHDV effectiveness. Rabbits form highly distinct breeding groups that typically consist of up to three males and nine females that maintain strong social bonds (Surridge et al. 1999). Various studies in different countries using direct observation and radio-tracking have suggested that interactions among rabbits within a social group occur commonly and individuals from neighbouring social groups also interact, although less frequently than group members (Cowan 1987a; Gibb 1993; Williams et al. 1995). However, the availability of proximity loggers means that information on social interactions of rabbits that occur both above ground as well as inside warren systems can be collected at a level of detail previously not possible. Here, we quantify intra- and inter-group contact rates and determine the extent of spatial and temporal heterogeneities in the social organisation of free-ranging wild rabbits. Specifically, we predict that there will be heterogeneities in contact behaviour (1) between different populations living in habitats with different characteristics likely to affect rabbit social organisation, (2) between sexes and groups over time according to breeding patterns, and (3) between individuals within and between groups.

Materials and methods

Study sites

The fieldwork was carried out in the Central Tablelands of New South Wales, between Orange and Bathurst (33°24′ 40″ S, 149°22′00″ E). We used two sites, Oaky Creek and Valpine, which are less than 3 km apart but different in terms of habitat quality and resource availability. Both sites are at an altitude of 700–950 m and have an annual rainfall of approximately 500 mm during the study year. Within both study sites, rabbit breeding commenced in February after an increase in rainfall following the dry summer months and continued through the rest of the study year (M. Marsh, unpublished data).

Oaky Creek is an unmanaged site used infrequently for sheep grazing. The vegetation consists of patches of trees, shrubs and unpalatable grasses. The study site was a small part (c. 0.05 km²) of the 200-ha paddock. The majority of rabbits in Oaky Creek lived under the numerous bramble (*Rubus fruticosa* spp.) bushes that extended over large areas. Valpine is a more intensively managed site, with more uniform, abundant pasture throughout the year, used for sheep and cattle production. The study area in Valpine covered c. 0.05 km² and has rabbit burrows which were distributed in four parallel gullies c. 50 m apart. Neither site had a history of substantial rabbit control prior to the study. In Oaky Creek, RHDV has been detected on various occasions, but its impacts have been restricted to single warren systems rather than the whole site. In Valpine, RHDV epidemics have been more successful in reducing rabbit numbers in the past (Glen Saunders, personal communication).

Proximity loggers

We used proximity loggers (Sirtrack Ltd., Havelock, NZ) to record direct contacts among rabbits. These loggers have previously been used on other mammal species (Ji et al. 2005; Prange et al. 2006; Swain and Bishop-Hurley 2007; Böhm et al. 2009), and the accuracy of the loggers has been confirmed and quantified in both laboratory and field settings (Prange et al. 2006; Böhm et al. 2009).

The data logger units, which weighed less than 20 g (2% of the body weight of our smallest collared rabbit), were attached to the rabbits using a neck collar. The loggers transmit unique identification codes via a UHF transceiver within 1.5-s intervals while simultaneously "listening" for other loggers within a pre-defined detection range. Once another logger is detected, data are recorded until the contact is broken for the length of a pre-defined "separation time" (30 s in this study). Logger ID, date, start time and duration of the recorded contact of the transmitting unit are then stored in the logger memory.

Prior to use in the field, all loggers were tested in a laboratory and their detection range was set to 50–100 cm (equivalent to power setting 32). Since contact distances are reduced by around 50% in the field compared with laboratory tests (Böhm et al. 2009), this setting ensured that we would be recording only close contacts whilst minimising the likelihood of missing contacts completely. Each proximity logger emits a VHF signal transmitting at 150 MHz, which allows their location in the field. The logger battery life was 5–6 months for most collars.

Rabbit trapping and collaring

Trapping was carried out in both sites once every season throughout the study year (summer, December–

February; autumn, March–May; winter, June–August; spring, September–November). At each site, a total of 100 traps was used during each trapping session. Traps were placed at least 5 m apart from each other near every active warren, and the number of traps near a warren was increased with warren size up to a maximum of 20 traps per warren. We aimed to conduct the trapping sessions over five consecutive days. Before every trapping session, pre-baiting was conducted on three occasions: 5, 3 and 2 days before the first trap night.

Rabbits were trapped in wire cages baited with diced carrot. The traps were set at dusk and checked the next morning. New captures within each trapping session were sexed, weighed and inspected for presence of fleas, abnormalities and clinical signs of myxomatosis. Blood samples were taken from a random selection of captures during each trapping session for the detection of RHDV outbreaks (see "Electronic Supplementary Material", Fig. S1). The reproductive status of females was also recorded. A pair of metal ear tags containing a unique identification code was attached to the ears of all newly captured rabbits. ID numbers of all recaptures were noted for the capture–mark–recapture analysis (see "Electronic Supplementary Material", Appendix S1).

Proximity loggers were fitted on a random selection of those adult rabbits caught that weighed more than 1 kg. When a collared rabbit died, the proximity logger was recovered from the field and fitted on a new rabbit during the next trapping session. Altogether, 126 rabbits were fitted with proximity loggers at least once during the study. Proximity data collection was carried out in two separate data periods: December 2006–April 2007 (summer and autumn; data period 1) and September 2007–November 2007 (spring; data period 2) (Table 1).

Radio-tracking and defining social groups

Radio-tracking on foot using hand-held Yagi antennae was carried out during most weeks of the study year to monitor the survival of collared rabbits and to collect data on their

Table 1 Total number of proximity loggers on male and female rabbits in Oaky Creek and Valpine during data period 1 (Dec 06–April 07) and data period 2 (Sept 07–Nov 07)

Site	Data period	Males	Females	Total
Oaky Creek	1	22	25	47
	2	14	13	27
Valpine	1	21	23	44
	2	11	16	27
Total		68	77	145

space use. Radio-tracking effort was distributed evenly across day and night, and locations were recorded using a hand-held GPS. To minimise autocorrelation in the radio-tracking data, location fixes for a rabbit were separated by at least 1 h and a maximum of four fixes was collected per 24 h. This protocol, designed to obtain a representative sample of movement over the periods of analysis (White and Garrott 1990), was in line with previous studies on rabbit social organisation in the area (White et al. 2003). The 1-h time interval is sufficient to avoid temporal autocorrelation, being well in excess of the time taken by an average individual rabbit to traverse its home range and using a maximum of four fixes per 24 h minimises any potential influence of specific time periods on overall home range estimates.

Rabbit warrens within the study sites did not have clear boundaries on the ground. Consequently, a priori allocation of rabbits into social groups on the basis of capture site was not considered to be reliable. Instead, following the approach of White et al. (2003) for the same study area, we based our initial allocation of rabbits into social groups on evidence from radio-tracking data. Based on our radio-tracking data, we identified three categories of rabbits. Firstly, we had 12 rabbits whose 95% minimum convex polygons (MCP) home ranges (estimated from inactive day-time fixes) did not overlap with any others. These rabbits were defined as being outside the social group structure and were excluded from the subsequent analysis. This left us with 145 out of an original 157 rabbits. For 137 of these remaining rabbits, we were able to define asymptotic home ranges based on 95% MCP estimated from inactive daytime fixes. These rabbits were very faithful to specific warren clusters and could therefore be allocated confidently to specific social groups on the basis of home range overlap patterns. Finally, we had eight rabbits (one in Oaky Creek during data period 1, five in Valpine during data period 1, and one in each of Oaky Creek and Valpine during data period 2) for which we had insufficient inactive fixes to provide reliable 95% MCP home ranges and hence could not be allocated to specific groups confidently based on radio-tracking alone. The majority of our radio-tracking data and field observations indicated clearly that social groupings were present, so it was important to determine the group to which these rabbits belonged. To do this, we used cluster analysis based on the proximity data. We created a similarity matrix from the presence and absence of contacts between each pair of rabbits using the Bray–Curtis coefficient (Zuur et al. 2007). We then used non-metric multidimensional scaling to confirm the exclusion of rabbits with no overlapping minimum convex polygons from the social groups (12 rabbits altogether throughout the study as mentioned above). For the cluster analysis, a dissimilarity value of 0.87 best represented the social group

allocation that we had made for the 137 rabbits with sufficient radio-tracking data (see "Electronic Supplementary Material", Fig. S2). We therefore used average linkage cluster analysis based on this cutoff value to confirm the allocation of the eight individuals with scarce radio-tracking data to social groups.

Data analysis

Home range overlap between social groups

Home range estimates were made in ArcView 3.2 using the 'Animal Movement' extension (Hooge and Eichenlaub 2000). To investigate space use of rabbit social groups, all radio-tracking data (including night-time fixes) recorded for rabbits belonging to the same social group were combined and 95% minimum convex polygons were calculated. This method makes no assumptions about the distribution of fixes and provides a more conservative estimate of the total area used than 100% minimum convex polygons (Boitani and Fuller 2000). The potential for interaction between individuals from different social groups was estimated by calculating their home range overlap as a percentage of the total area covered by their combined 95% minimum convex polygon home ranges.

Proximity data sorting

Prior to proximity data analysis, we removed all contacts recorded during trapping periods. The beginning of a trapping session was defined as sunset in the evening when traps were first opened, and the end of trapping session was defined as the average release time on the last trapping day (12 h after last trap opening). We also removed the first 12 h of data recorded after the end of each trapping session.

Throughout the study, several collared rabbits were lost to predation, other causes of mortality and emigration. In these circumstances, the date when a rabbit was last known alive within the study area (as determined by regular radio-tracking) was taken as the last date of data recording. This way, the amount of data was maximised without risking an accumulation of false contacts. In the event of logger battery failure (usually after 5–6 months of data recording), the last recorded contact was taken as the last day of battery life. During data period 1, most logger batteries had been exhausted by mid May 2007, so all data recorded after April 2007 were excluded from the analysis.

Because proximity loggers tend to record extended-duration contacts as multiple events (Prange et al. 2006), we combined the "broken" contacts that occurred within less than the pre-defined separation time (30 s). Of all recorded contacts, 37% lasted for 1 s, which is typical for proximity logger data (Ji et al. 2005; Prange et al. 2006;

Böhm et al. 2009). Following the protocol from Böhm et al. (2009), all 1-s contacts were omitted from the analysis. Finally, in order to reduce spatial correlation in the analysis, contact data were divided into intra-group contacts (occurring among rabbits from the same social group) and inter-group contacts (occurring among rabbits from different social groups).

Intra- and inter-group contact measures

To standardise the contact measures between individuals, mean daily intra-group contact frequency C_{Freq} and daily intra-group contact duration C_{Dur} (in seconds) were calculated for each rabbit, based on the total number of contacts and the total contact duration divided by the number of days for which the proximity logger was attached. Each daily contact frequency and duration estimate was then divided by the number of individuals available for contact within the rabbit's social group at any one time (i.e. the number of individuals within a social group wearing proximity loggers on that day). Therefore, intra-group C_{Freq} and C_{Dur} represent the average daily contact frequency and duration for a specific rabbit with any other collared individual within its social group on any one day. Thus, they are measures of contact behaviour per collar available rather than total measures. Prior to statistical analysis, intra-group C_{Freq} was cubic root-transformed and C_{Dur} was quadratic root-transformed to gain normality and homogeneity of variances.

Daily inter-group contact frequency and duration were calculated similarly, with the exception of dividing the daily inter-group contact frequency and duration estimates by the number of rabbits available for contact outside the individual's social group at any one day. Because inter-group contacts were infrequent, only the intra-group contacts were analysed statistically.

Statistical analysis

The analysis of intra-group contacts was performed in the 'R' statistical programming environment (R Development Core Team 2009). Pearson's correlations were performed on the transformed C_{Freq} and C_{Dur} in order to assess the consistency of data logging. Linear mixed-effects (LME) modelling was then applied to investigate the differences in C_{Freq} and C_{Dur} within each data period using the 'lnme' package (Pinheiro et al. 2008) in R. LME allows the analysis of hierarchically structured data with both fixed and random coefficients and multiple error terms (Zuur et al. 2007) and was suitable for our analysis of daily contact frequency and duration that were repeatedly sampled from the same rabbits and social groups. The random error structure was fitted using restricted log-likelihood (REML)

for the C_{Freq} and C_{Dur} for each data period. It included a random intercept for rabbit ID for all models except C_{Freq} model for data period 1, which included both rabbit ID and social group as random factors. The fixed factors included in the model selection were sex, time of day (daytime after sunrise and before sunset), site and month. The fixed components of the selected model were optimised using maximum likelihood (Burnham and Anderson 2002), while the results of the most optimal model (sensu Zuur et al. 2007) were presented with REML (Zuur et al. 2007). Inspection of correlation in residuals justified the exclusion of autocorrelation structures in the models.

Results

Home range overlap between social groups

The mean home range overlap between the social groups was 50% for Oaky Creek and 45% for Valpine during data period 1 (Fig. 1). The group home ranges overlapped less during data period 2 (10% in Oaky Creek and 5% in Valpine).

Proximity logger returns

Due to rabbit population fluctuations as well as losses and additions of collared rabbits in the field, the percentage of adult rabbits collared varied between 29% and 87% in Oaky Creek and between 21% and 68% in Valpine (Table 2; see "Electronic Supplementary Material", Fig. S1). The proximity loggers were recovered from 91% and 96% of collared rabbits in Oaky Creek and 93% and 96% of collared rabbits in Valpine for data periods 1 and 2, respectively. Three loggers had recorded no data, all of which were on rabbits that did not belong to a social group.
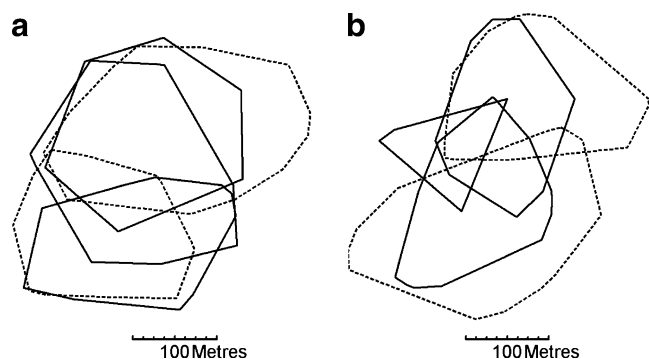

Fig. 1 Overlap of home ranges between rabbit social groups in **a** Oaky Creek and **b** Valpine. *Solid lines* show group home ranges for data period 1 and *dotted lines* for data period 2

Table 2 Percentage of the total population and adult population included in the contact data analysis in Oaky Creek and Valpine within each season during each data period. No proximity data were collected between May and August (Dec–Feb, summer; Mar–May, autumn; Sept–Nov, spring)

Site	Data period	Season	Total population, %	Adults, %
Oaky Creek	1	Summer	26–31	29–35
	1	Autumn	50–70	60–87
	2	Spring	21–28	35–50
Valpine	1	Summer	17–24	21–31
	1	Autumn	15–28	33–57
	2	Spring	21–29	37–68

The other nine transient rabbits had recorded highly infrequent contacts and were excluded from the analysis of intra- and inter-group contact behaviour. Four loggers (two pairs) ran out of memory space during data period 1 in Valpine, all of which were recovered and downloaded within a week from them becoming full. Altogether, the proximity loggers recorded 110,221 intra-group contacts representing a total duration of 3,946 h, and 73 (38 min) inter-group contacts were recorded.

Intra-group contacts

All rabbits included in the analysis made contacts with rabbits in their social groups. We recorded within-individual variation in contact rate and duration over the data periods (Fig. 2a–d). Mean intra-group C_{Freq} was 1.54± 0.23 (SE) contacts/day, and mean intra-group C_{Dur} was 202± 38 s/day (Table 3). However, both measures were positively skewed as indicated by the large differences
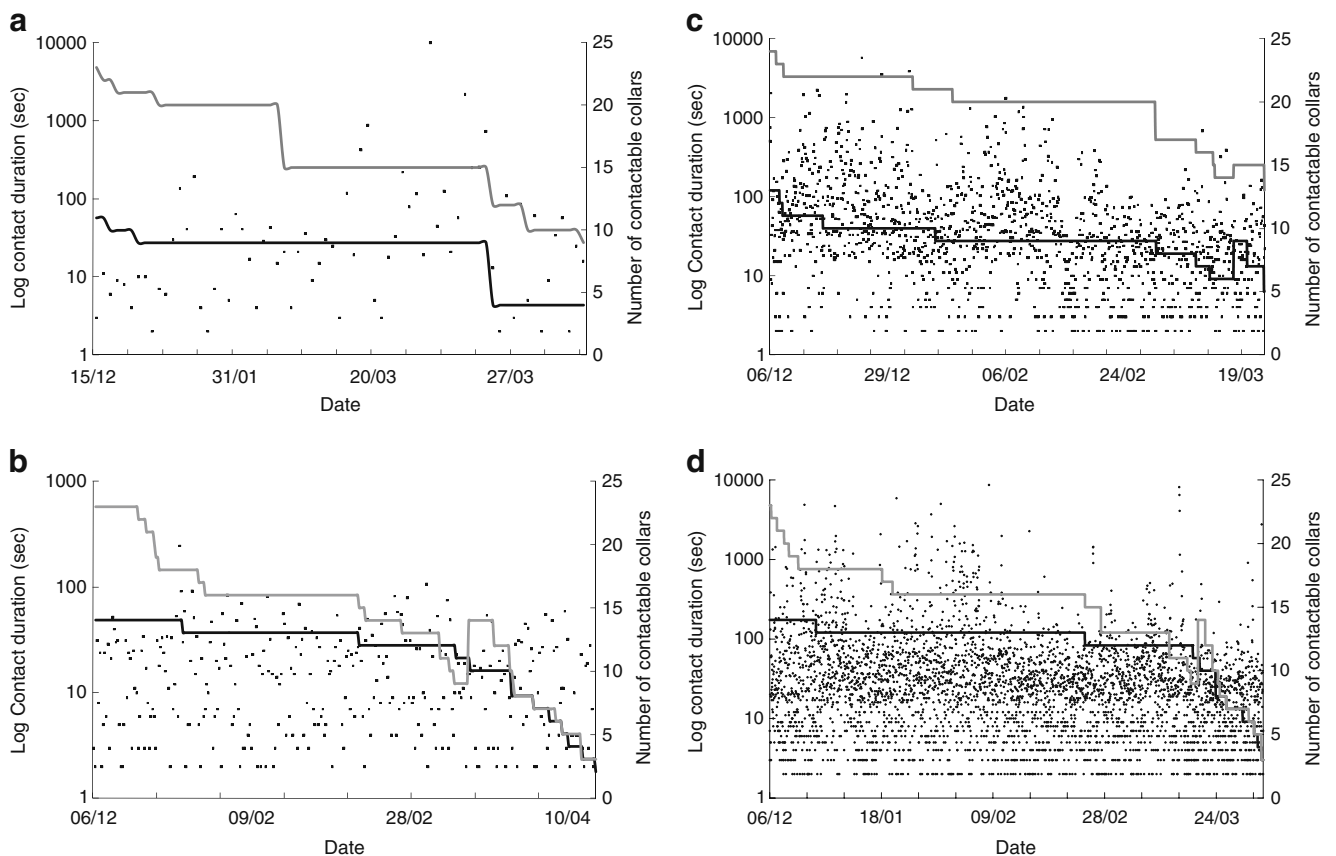

Fig. 2 Log duration (in seconds) of each contact made by selected individual male rabbits at the study sites. Each *dot* represents the log duration of single contact. The changes in the number of contactable collars within the individual's social group (*black line*) and outside its social group (*grey line*) over the data period are also shown. **a** Male rabbit (ID 30), Oaky Creek, data period 1, a total of 72 contacts, of which two were inter-group contacts lasting for 9 s in total. **b** Male rabbit (ID 8), Oaky Creek, data period 1, a total of 317 contacts, of which none were inter-group contacts. **c** Male rabbit (ID35), Oaky Creek, data period 1, a total of 1,470 contacts in total, of which none were inter-group contacts. **d** Male rabbit (ID 27), Oaky Creek, data period 1, a total of 3,980 contacts, of which two were inter-group contacts lasting for 4 s in total

Table 3 Mean (standard error; SE) and median (semi-interquartile range; SIQR) C_{Freq} and C_{Dur} (in seconds) for intra- and (b) inter-group contacts in Oaky Creek and Valpine for the two data periods

Site	Data period	Mean C_{Freq} (SE)	Median C_{Freq} (SIQR)	Mean C_{Dur} (SE)	Median C_{Dur} (SIQR)
Intra-group contacts					
Oaky Creek	1	0.92 (0.17)	0.43 (0.65)	77 (17)	33 (49)
	2	1.26 (0.30)	0.65 (0.88)	142 (61)	26 (35)
Valpine	1	1.68 (0.31)	0.27 (0.79)	288 (54)	10 (92)
	2	2.50 (0.78)	0.80 (2.00)	326 (110)	54 (226)
Total		1.54 (0.23)	0.54 (0.84)	202 (38)	29 (85)
Inter-group contacts					
Oaky Creek[a]	1	0.0003 (0.0001)	0	0.003 (0.002)	0
	2	0.0008 (0.0007)	0	0.007 (0.006)	0
Valpine[b]	1	0.0006 (0.0003)	0	0.010 (0.006)	0
	2	0.0007 (0.0005)	0	0.008 (0.006)	0
Total		0.0007 (0.0004)	0	0.007 (0.004)	0

[a] The mean values are based on 26 rabbits, of which 14 made inter-group contacts

[b] The mean values are based on 26 rabbits, of which 15 made inter-group contacts

between the mean and median estimates. The intra-group C_{Freq} ranged from 0.004 to 12.0 contacts/day and C_{Dur} from 0.01 s to 3.5 h/day. The frequency of high and low intra-group C_{Freq} estimates in the rabbit populations also varied between the study months (Fig. 3). Intra-group C_{Freq} and C_{Dur} decreased with increasing seasonal rabbit abundance within the study sites, although because both measures are adjusted for the availability of collars a decrease in individual contact rates does not necessarily represent a decline in the total contact rate across the population. Both intra-group contact measures were higher in Valpine than in Oaky Creek for all seasons (Fig. 4; see "Electronic Supplementary Material", Fig. S1 and Table S1, for further information on rabbit abundance).

Significant positive correlations were found between intra-group C_{Freq} and C_{Dur} for both data periods (data period 1: $r=0.956$, d.f.=512, $P<0.001$; data period 2: $r=0.949$, d.f.=200, $P<0.001$; Fig. 5). The optimised fixed structures in the LME models based on cube root-transformed intra-group C_{Freq} and C_{Dur} were similar for both data periods (Tables 4 and 5). Sex was not a significant factor and was therefore not included in the most optimal structures for any of the models. Time of day was also not included in the most optimal model for C_{Freq} (data period 1) and C_{Dur} (data period 2). Month was a significant factor for both data periods for C_{Freq} (data period 1 LME: $F_{Month}=2.926$, d.f.=4, $P<0.05$; data period 2 LME: $F_{Month}=15.566$, d.f.=2, $P<0.001$) and for C_{Dur} for data period 2 (LME: $F_{Month}=8.727$; d.f.=2, $P<0.001$). In addition, for both data periods, there was a significant site–month interaction for C_{Freq} (data period 1 LME: $F_{Month:Site}=5.249$, d.f.=4; $P<0.001$; data period 2 LME: $F_{Month:Site}=7.710$, d.f.=2; $P<0.001$) and C_{Dur} (data period 1 LME:

$F_{Month:Site}=4.746$, d.f.=4; $P<0.001$; data period 2 LME: $F_{Month:Site}=4.362$, d.f.=2; $P<0.05$). C_{Dur} was significantly higher during daytime than night-time during data period 1 (LME: $F_{Time\ of\ day}=10.955$, d.f. = 1; $P<0.001$). For data period 2, C_{Freq} was significantly higher during night-time (LME: $F_{Time\ of\ day}=8.035$, d.f.=1; $P<0.01$).

Inter-group contacts

The mean inter-group C_{Freq} was 0.0007 ± 0.0004 (SE) (median=0) contacts per day and mean C_{Dur} was 0.007 s ±0.004 (SE) (median=0) (Table 3). Most inter-group contacts were short in duration (<1 min), and female–male contacts were the most frequent within both sites and data periods (Fig. 2a, data period 2 not shown). During data period 1, inter-group contacts were more common and longer in total duration in Valpine ($N=42$, total duration= 588 s) than in Oaky Creek (data period 1, $N=20$, total duration=203 s) (Fig. 6). Fourteen rabbits in Oaky Creek and fifteen in Valpine were involved in these interactions, and the majority of the contacts occurred at night-time (74% in Oaky Creek, 61% of total duration; 87% in Valpine, 52% of total duration). During data period 2, only four inter-group contacts (total duration=39 s) were recorded in Oaky Creek and seven (total duration=91 s) in Valpine (data not shown).

Discussion

Our use of proximity loggers in this study has enabled the first quantification of intra- and inter-group contact frequency of free-ranging wild rabbits within and between

Fig. 3 Frequency histograms for C_{Freq} estimates for all rabbits in Oaky Creek (in *black*) and Valpine (in *grey*) for **a** December 2006, **b** January 2007, **c** February 2007, **d** March 2007, **e** April 2007, **f** September 2007, **g** October 2007 and **h** November 2007
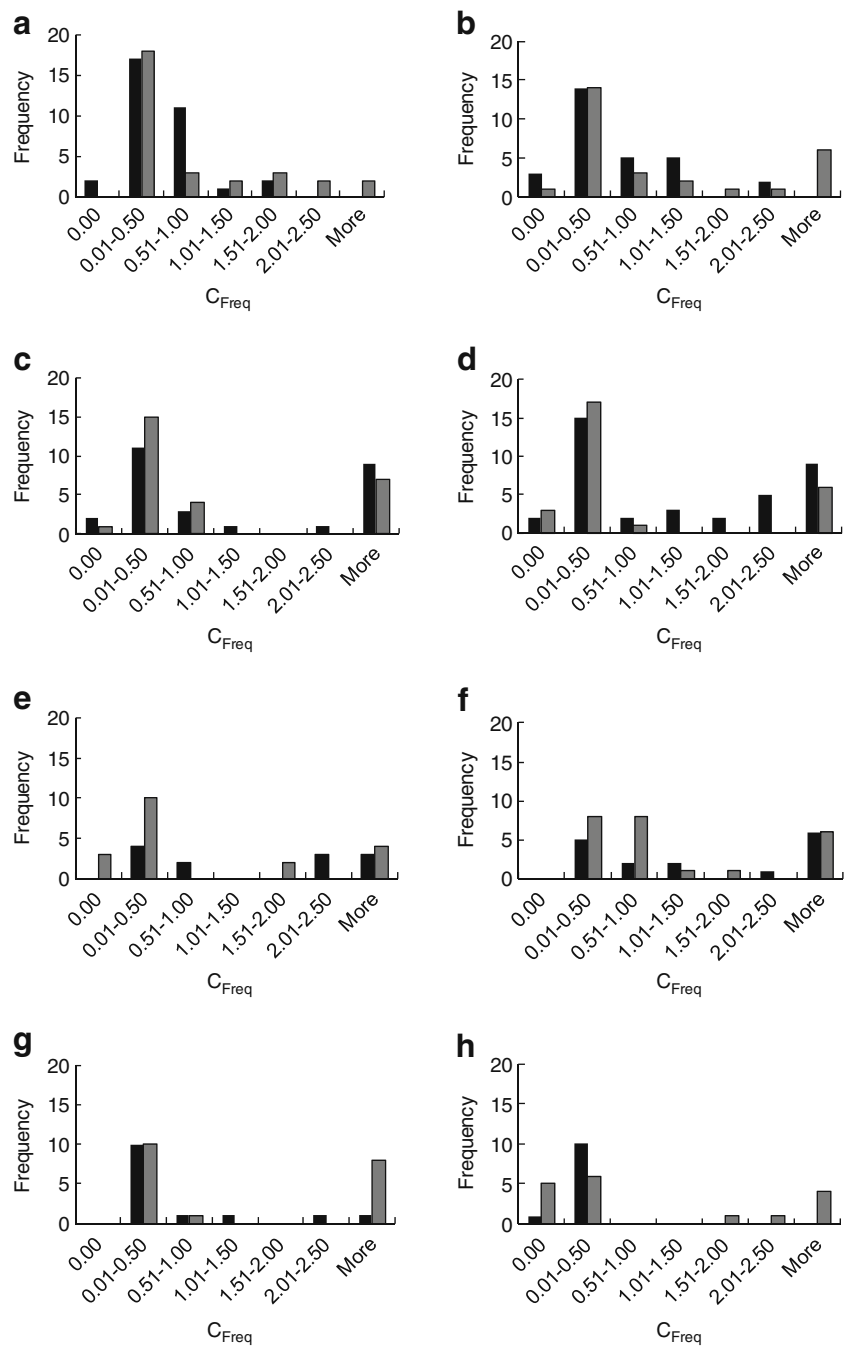

Fig. 4 Relationship between **a** mean C_{Freq} (±SE) and **b** mean C_{Dur} (±SE) and abundance of adult rabbits for Oaky Creek (in *black*) and Valpine (in *grey*). The variables were calculated for each study season (summer, autumn, spring). See "Electronic Supplementary Material" for further details on abundance estimates
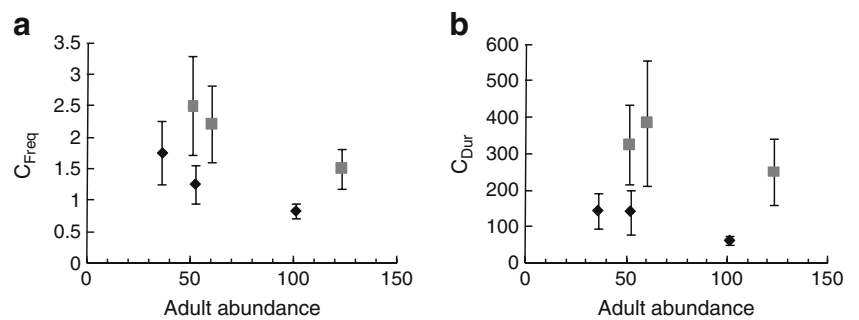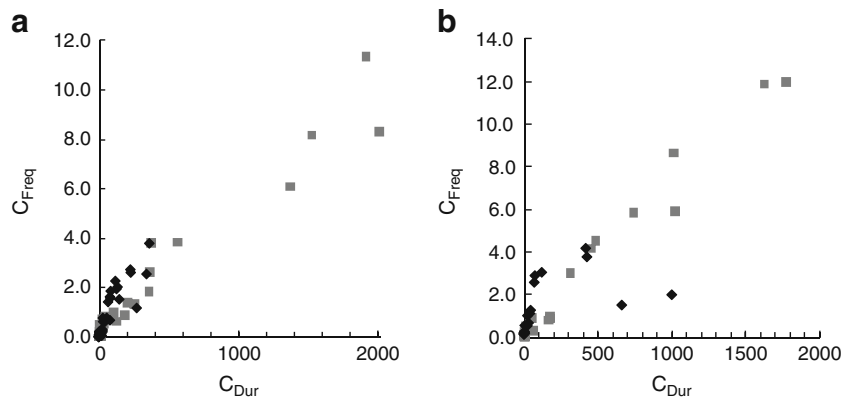
individuals and populations. These data have highlighted spatial and temporal heterogeneities in the social organisation of rabbits between populations and between and within social groups in the same population.

Intra-group contacts

Intra-group interactions among rabbits fitted with proximity loggers were less frequent than we expected based on previous research. Even though we recorded a large number of intra-group interactions overall and all rabbits within a social group made contacts with at least some of the other group members, contacts among rabbits sharing warrens, food resources and social associates were relatively infrequent when standardised to take into account the number of data recording days and collared rabbits within any given day in the social groups. On average, a rabbit made only 1.54±0.23 (SE) (median=0.54) intra-group

contacts per day with the other rabbits in its social group which were fitted with a proximity logger, lasting for 202± 38 s (SE) (median=29 s) (Table 3).

Our findings also demonstrated the presence of substantial heterogeneities in the daily intra-group contact rate and duration within and between individuals (Figs. 2a–d and 3). Even though most rabbits made relatively few contacts with collared rabbits in their social groups over time (for example, Fig. 2a), some made contacts with each other extremely frequently (for example, Fig. 2d). Rabbits with low average daily intra-group contact frequency and/or duration (min C_{Freq} =0.004 contacts/day, min C_{Dur}= 0.01 s/day) may be socially displaced individuals living on the periphery of their social groups. Although these individuals may still be sharing resources and associates with other members of the social group, they are less involved in social interactions within the group. These rabbits may correspond to "surface dwellers", which have previously been identified in

Table 4 Anova tables indicating the significance of fixed effects for the linear mixed-effects models for differences in the intra-group daily contact frequency (C_{Freq}) and duration (C_{Dur}, in seconds) for (a) data period 1 and (b) data period 2. Factors considered are: site (Oaky Creek, Valpine), month (Dec, Jan, Feb, Mar, Apr (data period 1); Sept,

Oct, Nov (data period 2)), and Time of day (night-time, daytime). For both models, sex (male, female) and the 3-way interaction (site-month-time of day) were left out during the model selection procedure. Additionally, time of day was not in the optimal fixed structure for C_{Freq} for data period 1 and C_{Dur} for data period 2

Model 1: C_{Freq}				Model 2: C_{Dur}			
	DF	F-value	P		DF	F-value	P
(a)							
Intercept	436	47.41	<0.001***	Intercept	435	148.48	<0.001***
Site	4	0.22	0.663	Site	68	0.62	0.436
Month	436	2.93	<0.05*	Month	435	1.18	0.318
Time of day	–	–	–	Time of day	435	10.96	<0.001***
Site:Month	436	5.25	<0.001***	Site:Month	435	4.75	<0.001***
(b)							
Intercept	150	134.56	<0.001***	Intercept	151	108.06	<0.001***
Site	45	0.63	0.511	Site	45	1.19	0.282
Month	150	15.57	<0.001***	Month	151	8.73	<0.001***
Time of day	150	8.04	<0.01**	Time of day	–	–	–
Site:Month	150	7.71	<0.001***	Site:Month	151	4.36	<0.05*

***P<0.001; **P<0.01; *P<0.05

Table 5 Random and fixed effects with coefficient values from the linear mixed-effects models for differences in the intra-group daily contact frequency (C_{Freq}) and duration (C_{Dur}, in seconds) for (a) data period 1 and (b) data period 2. Factors considered are: site (Oaky Creek, Valpine), month (Dec, Jan, Feb, Mar, Apr (data period 1); Sept, Oct, Nov (data period 2)), and time of day (night-time, daytime). For both models, sex (male, female) and the 3-way interaction (site-month-time of day) were left out during the model selection procedure. Additionally, time of day was not in the optimal fixed structure for C_{Freq} for data period 1 and C_{Dur} for data period 2. Results are shown relative to reference category (site = Oaky Creek; month = December (data period 1), September (data period 2); time of day = night-time; site-month = Oaky Creek:December (data period 1), Oaky Creek:September (data period 2))

Variable	Model1: C_{Freq}				Model2: C_{Dur}			
(a)								
Random effects:								
	Intercept	Residual			Intercept	Residual		
Std dev	0.36	0.25			1.21	0.84		
Fixed effects:								
	Coeff.±SE	DF	t	P	Coeff.±SE	DF	t	P
(Intercept)	0.52±0.13	436	3.98	<0.001***	1.57±0.23	435	6.86	<0.001***
Site								
VP	0.16±0.19	4	0.83	0.455	0.43 ±0.33	68	1.31	0.196
Month								
Jan	0.01±0.05	436	0.10	0.918	−0.11±0.16	435	−0.73	0.464
Feb	0.12±0.05	436	0.42	<0.05*	−0.05±0.16	435	−0.31	0.760
Mar	0.16±0.05	436	3.23	<0.01**	0.20±0.17	435	1.18	0.240
Apr	0.20±0.07	436	2.88	<0.01**	0.24±0.22	435	1.09	0.278
Time of day								
Daytime	–	–	–	–	0.25±0.07	435	3.32	<0.001***
Site:Month								
VP:Jan	0.03±0.07	436	0.38	0.707	0.02±0.22	435	0.10	0.918
VP:Feb	−0.01±0.07	436	−0.15	0.881	0.17±0.23	435	0.76	0.449
VP:Mar	−0.22±0.07	436	−0.19	<0.01**	−0.64±0.23	435	−0.75	<0.01**
VP:Apr	−0.25±0.09	436	−0.84	<0.01**	−0.75±0.29	435	−2.57	<0.01**
(b)								
Random effects:								
	Intercept	Residual			Intercept	Residual		
Std dev	1.41	0.23			1.31	0.77		
Fixed effects:								
	Coeff.±SE	DF	t	P	Coeff.±SE	DF	t	P
(Intercept)	0.91±0.10	150	9.11	<0.001***	2.28±0.32	151	7.18	<0.001***
Site								
VP	−0.06±0.13	45	−0.48	0.637	0.04±0.43	45	0.10	0.923
Month								
Oct	−0.32±0.08	150	−4.27	<0.001***	−0.61±0.25	151	−2.44	<0.05*
Nov	−0.45±0.08	150	−5.71	<0.001***	−1.19±0.26	151	−4.56	<0.001***
Time of day								
Daytime	−0.09±0.03	150	−2.84	<0.01**	–	–	–	–
Site:Month								
VP:Oct	0.35±0.09	150	3.784	<0.001***	0.72±0.31	151	2.37	<0.05*
VP:Nov	0.29±0.10	150	3.00	<0.001**	0.89±0.32	151	2.79	<0.01**

Breeding within both study sites commenced in mid February and carried on for the rest of the study year

VP Valpine; *SE* standard error; *DF* degrees of freedom

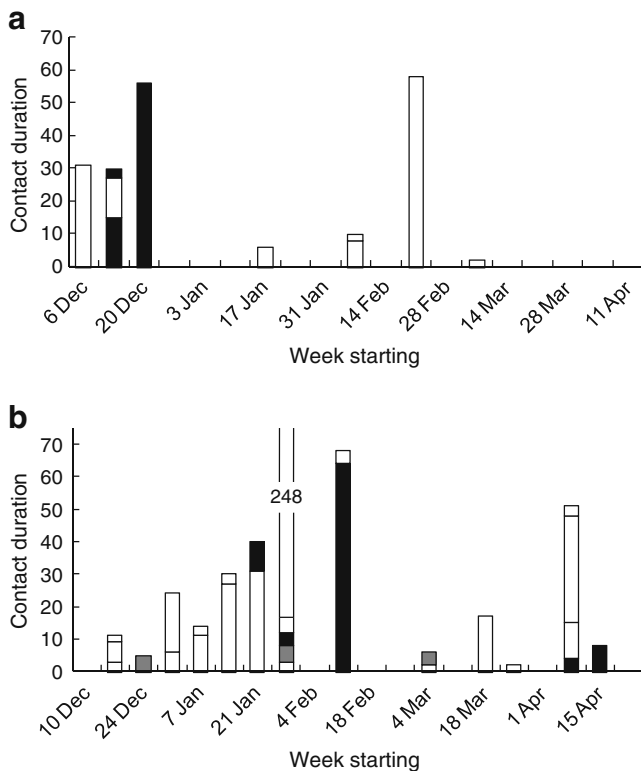***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

Fig. 6 Inter-group contact profiles over time, showing the cumulative duration (in seconds) of contacts in **a** Oaky Creek and **b** Valpine during data period 1. Each contact is shown for female–male (in *white*) and male–male (in *black*) and female–female (in *grey*) pairs separately. Each segment within a *bar* represents a different pair of individual rabbits. The data are summarised per week

several rabbit populations (King et al. 1984; Gibb 1993; White et al. 2003). The unusually high average daily contact frequency and duration (max C_{Freq} =12.0 contacts/day, max C_{Dur}=3.5 h/day) are most likely to occur between breeding pairs which typically exist within rabbit warren systems (Gibb 1993). These individuals formed a minority of the rabbits in this study and were more common in Valpine than in Oaky Creek (Fig. 5).

In addition to the heterogeneities in intra-group contact rates within and between individuals, we recorded significant diurnal and seasonal variations in the average daily intra-group contact rates (Table 5). For example, within both sites, C_{Freq} was significantly lower during the early summer months (December and January) than during autumn. As the start of the breeding season (February) coincided with an increase in the frequency of high daily contact rates in the collared rabbit populations (Fig. 3; also see Fig. 2a–d for changes in contact rates for individuals), the temporal variation in contact behaviour is likely to be related to increased activity during breeding. Temporal heterogeneity in rabbit activity has also been recorded in various radio-tracking studies (Gibb 1993; Moseby et al. 2005). We also recorded significant differences in the

average daily contact frequency and duration between sites over time (Table 3; Fig. 4), which may be driven by site-specific factors such as resource availability, habitat quality, population density and social group sex and/or age structure.

Inter-group contacts

Various radio-tracking studies have shown a regular occurrence of home range overlap between rabbits from neighbouring social groups, which suggests potential for frequent inter-group interactions (Gibb 1993; White et al. 2003). Even though our study also showed a high percentage of home range overlap between neighbouring social groups especially during data period 1 (Fig. 1), inter-group contacts were extremely infrequent despite the close vicinity of social groups and small size of the study areas (Table 3). On average, only 0.0007±0.0004 (SE) (median= 0) inter-group contacts were made per day, lasting for 0.007± 0.004 s (SE) (median=0). The highly uncommon occurrence of inter-group contacts suggests that wild rabbits may avoid close contact with individuals from different social groups. Cowan (1987a) also recorded rare occurrence of inter-group interactions during direct observations at daytime; however, our study is the first to quantify this conclusively without potential biases caused by limited sampling periods or disturbance during observations.

The inter-group contacts that did occur revealed further heterogeneities in the contact behaviour of rabbits. For example, only a small proportion of the collared rabbits made inter-group contacts, and intersexual encounters between social groups, presumably sexual of nature (Cowan 1987a), were more common and lasted for longer than intrasexual interactions (Fig. 6). The rarity of inter-group interactions between male–male and female–female pairs indicates a low occurrence of territorial encounters, thus providing empirical data to confirm a suggestion made by a previous study based on patterns of home range overlaps (White et al. 2003). Furthermore, inter-group contacts were more common in Valpine than in Oaky Creek, which may be due to less distinct social groups or more intense competition for mates and warrens.

Implications for disease transmission in rabbit populations

The outcome of an epidemic spreading directly though a contact network relies on both relatively frequent local (within-group) and occasional global (between-group) population mixing (Ball et al. 1997). Consequently, the social organisation of a host population can have important implications for the impact of infectious disease which is transmitted wholly or in part via direct contacts between individuals. Our quantification of intra- and inter-group

contact rate (for the given the sampling intensity) among free-ranging wild rabbits can be directly applied to aid the parameterisation of mathematical models on the direct transmission of infectious diseases such as RHDV in rabbit populations. This is likely to improve the predictive power of epidemiological models on the rabbit–RHDV system, which traditionally have assumed homogeneous mixing of individuals (Barlow and Kean 1998; Barlow et al. 2002). However, direct transmission of a pathogen not only depends on contact rates but also requires one of the interacting individuals to be infected and the other susceptible, and the probability of infection resulting from such "appropriate" contacts also affects the outcome of the interaction (McCallum et al. 2001). A complete quantification of direct pathogen transmission based on empirical data in rabbits or any other wildlife host therefore remains to be achieved.

The variations in contact structure we have observed could contribute towards the observed patchy RHDV effectiveness in Australia and make the management of RHDV in southern Europe more problematic. The presence of heterogeneity in daily intra- and inter-group contact behaviour may have a crucial role in disease dynamics and could ultimately determine the outcome of an epidemic (Lloyd-Smith et al. 2005). Additionally, the higher past effectiveness of RHDV in Valpine may be influenced by the less variable intra-group contact rates over time and the more frequent interactions between rabbit social groups observed in this study, as both may create more opportunities for direct disease spread. We also detected a slight decline in daily contact frequency and duration of rabbits with increasing rabbit abundance (Fig. 4). This is contrary to the assumptions of many disease models which assume density-dependent contact rates, but empirical data have shown similar patterns in other social mammals (Böhm et al. 2009). This suggests that the social structure of rabbits may be more stable at high densities and also has implications for the transmission dynamics of diseases based on direct contacts. The drivers for the differences in contact behaviour need to be further investigated, and even a relatively infrequent mixing of more distant individuals in a contact network may be enough for an epidemic to spread through a population (Kleczkowski and Grenfell 1999).

Since it was not justifiable to fit proximity collars on young rabbits for welfare reasons, this study was limited to quantifying the contact patterns of sub-adult and adult rabbits (>1 kg) only. Because kittens and juvenile rabbits may behave differently to mature rabbits, the intra- and inter-group contact rates reported here may represent a biased sample of the contact behaviour of rabbit populations. For example, even though young kittens are unlikely to move far from their home warrens (Kunkele and Von Holst 1996), they may be important in the intra-group contact behaviour. Juvenile rabbits may interact with individuals from neighbouring social groups more frequently than mature rabbits due to less established social ranking and dispersal from natal territories (Kunkele and Von Holst 1996). Such age-specific heterogeneities may also affect the rate of RHDV transmission in contact networks. Finally, as our study only measured direct contacts among collared rabbits, we cannot draw conclusions on the role of indirect transmission via insect vectors, latrines and carcasses in RHDV effectiveness despite their likely importance in the spread and persistence of the virus (Cooke and Fenner 2002).

Conclusions

Our study provides the first quantification of intra- and inter-group contact rates among wild rabbit. Intra-group contacts were rarer than we expected based on the previous assumptions on the highly sociable nature of rabbits. Inter-group interactions were extremely infrequent and brief despite the considerable home range overlap between the social groups. We also found considerable spatial and temporal heterogeneities in the contact patterns of wild rabbits within and between individuals and evidence for a decline in contact rates with increasing density, which is contrary to the assumptions of many disease models. Data such as these can be used to aid the parameterisation of mathematical models on the direct transmission of diseases such as RHDV in rabbit populations. All else being equal, such heterogeneities in the social behaviour of rabbits are likely to lead to differences in the probability of disease transmission per unit time between individuals and may be a contributing factor in the variable effectiveness of RHDV in temperate regions of Australia. Future work should be targeted at identifying the ecological drivers of these heterogeneities.

References

Andreasen V, Christiansen FB (1989) Persistence of an infectious disease in a subdivided population. Math Biosci 96:239–253

Ball F, Mollison D, Scalia-Tomba G (1997) Epidemics with two levels of mixing. Ann Appl Probab 7:46–89

Barlow ND, Kean JM (1998) Simple models for the impact of rabbit calicivirus disease (RCD) on Australasian rabbits. Ecol Modell 109:225–241

Barlow ND, Barron MC, Parkes J (2002) Rabbit haemorrhagic disease in New Zealand: field test of a disease–host model. Wildl Res 29:649–653

Böhm M, Palphramand KL, Newton-Cross G, Hutchings MR, White PCL (2008) Dynamic interactions among badgers: implications for sociality and disease transmission. J Anim Ecol 77:735–745

Böhm M, Hutchings MR, White PCL (2009) Contact networks in a wildlife–livestock host community: identifying high-risk individuals in the transmission of bovine TB among badgers and cattle. PLoS ONE 4:e5016

Boitani L, Fuller TK (2000) Research techniques in animal ecology. Controversies and consequences. Colombia University Press, New York

Burnham KP, Anderson DR (2002) Model selection and multimodel inference, 2nd edn. Springer, New York

Cooke BD, Fenner F (2002) Rabbit haemorrhagic disease and the biological control of wild rabbits, Oryctolagus cuniculus, in Australia and New Zealand. Wildl Res 29:689–706

Cowan DP (1987a) Aspects of the social organisation of the European wild rabbit (Oryctolagus cuniculus). Ethology 75:197–210

Cowan DP (1987b) Group living in the European rabbit (Oryctolagus cuniculus): mutual benefit or resource localization? J Anim Ecol 56:779–795

Delibes-Mateos M, Redpath SM, Angulo E, Ferrerasa P, Villafuerte R (2007) Rabbits as a keystone species in southern Europe. Biol Conserv 137:149–156

Delibes-Mateos M, Delibes M, Ferreras P, Villafuerte R (2008) Key role of European rabbits in the conservation of the Western Mediterranean Basin hotspot. Conserv Biol 22:1106–1117

Edwards GP, Pople AR, Saalfeld K, Caley P (2004) Introduced mammals in Australian rangelands: future threats and the role of monitoring programmes in management strategies. Austral Ecology 29:40–50

Gibb JA (1993) Sociality, time and space in sparse populations of rabbits (Oryctologus cuniculus). J Zool 229:581–607

Hooge N, Eichenlaub B (2000) Animal movement extension to Arcview, ver. 2.0. Alaska Science Center—Biological Science Office, US Geological Survey, Anchorage, AK, USA

Ji W, White PCL, Clout MN (2005) Contact rates between possums revealed by proximity data loggers. J Appl Ecol 42:595–604

King DR, Wheeler SH, Robinson MH (1984) Daytime locations of European rabbits at three localities in south-western Australia. Aust Wildl Res 11:89–92

Kleczkowski A, Grenfell BT (1999) Mean-field-type equations for spread of epidemics: the 'small world' model. Physica A 274:355–360

Kunkele J, Von Holst D (1996) Natal dispersal in the European wild rabbit. Anim Behav 51:1047–1059

Le Roux A, Cherry MI, Manser MB (2008) The effects of population density and sociality on scent marking in the yellow mongoose. J Zool 275:33–40

Lloyd-Smith JO, Schreiber SJ, Kopp PE, Getz WM (2005) Super-spreading and the effect of individual variation on disease emergence. Nature 438:355–359

Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM (2006) Quantifying the influence of sociality on population structure in bottlenose dolphins. J Anim Ecol 75:14–24

McCallum H, Barlow N, Hone J (2001) How should pathogen transmission be modelled? Trends Ecol Evol 16:295–300

McLeod S (2004) Counting the cost: impact of invasive animals in Australia 2004. Cooperative Research Centre for Pest Animal Control, Canberra

Meyers LA, Pourbohloul B, Newman MEJ, Skowronski DM, Brunham RC (2005) Network theory and SARS: predicting outbreak diversity. J Theor Biol 232:71–81

Mitani JC, Watts DP, Muller MN (2002) Recent developments in the study of wild chimpanzee behaviour. Evol Anthropol 11:9–25

Mollema L, Koene P, de Jong MCM (2006) Quantification of the contact structure in a feral cattle population and its hypothetical effect on the transmission of bovine herpesvirus 1. Prev Vet Med 77:161–179

Moreno S, Beltran JF, Cotilla I, Kuffner B, Laffite R, Jordan G, Ayala J, Quintero C, Jimenez A, Castro F, Cabezas S, Villafuerte R (2007) Long-term decline of the European wild rabbit (Oryctolagus cuniculus) in south-western Spain. Wildl Res 34:652–658

Moseby KE, De Jong S, Munro N, Pieck A (2005) Home range, activity and habitat use of European rabbits (Oryctolagus cuniculus) in arid Australia: implications for control. Wildl Res 32:305–311

Mutze G, Cooke B, Alexander P (1998) The initial impact of rabbit hemorrhagic disease on European rabbit populations in South Australia. J Wildl Dis 34:221–227

Newman MEJ (2002) Spread of epidemic disease on networks. Phys Rev E 66:1–11

Pinheiro J, Bates D, DebRoy S, Sarkar D, The R Core Team (2008) nlme: linear and nonlinear mixed effects models. R Package version 3.1-90

Prange S, Jordan T, Hunter C, Gehrt SD (2006) New radiocollars for the detection of proximity among individuals. Wildl Soc Bull 34:1333–1344

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rosell F, Gundersen G, Le Galliard JF (2008) Territory ownership and familiarity status affect how much male root voles (Microtus oeconomus) invest in territory defence. Behav Ecol Sociobiol 62:1559–1568

Schradin C (2004) Territorial defence in a group-living solitary forager: who, where, against whom? Behav Ecol Sociobiol 55:439–446

Surridge AK, Bell DJ, Hewitt GM (1999) From population structure to individual behaviour: genetic analysis of social structure in the European wild rabbit (Oryctolagus cuniculus). Biol J Linn Soc 68:57–71

Swain DL, Bishop-Hurley GJ (2007) Using contact logging devices to explore animal affiliations: quantifying cow–calf interactions. Appl Anim Behav Sci 102:1–11

Vonhof MJ, Whitehead H, Fenton MB (2004) Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. Anim Behav 68:507–521

White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data. Academic, London

White PCL, Harris S (1994) Encounters between red foxes (Vulpes vulpes): implications for territory maintenance, social cohesion and dispersal. J Anim Ecol 63:315–327

White PCL, Harris S, Smith GC (1995) Fox contact behaviour and rabies spread: a model for the estimation of contact probabilities between urban foxes at different population densities and its implications for rabies control in Britain. J Appl Ecol 32:693–706

White PCL, Newton-Cross GA, Gray M, Ashford R, White C, Saunders G (2003) Spatial interactions and habitat use of rabbits on pasture and implications for the spread of rabbit haemorrhagic disease in New South Wales. Wildl Res 30:49–58

Whitehead H (2009) SOCPROG programs: analysing animal social structures. Behav Ecol Sociobiol 63:765–778

Williams CK, Parer I, Coman B, Burley J, Braysher M (1995) Managing vertebrate pests: rabbits. Bureau of Resource Sciences and CSIRO Division of Wildlife and Ecology, Australian Government Publishing Service, Canberra

Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data. Springer, New York