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Original Investigation

Badger (*Meles meles*) contact metrics in a medium-density population

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ABSTRACT

Animal interactions are an important component of sociality in wildlife populations. Recent advances in technological and analytical applications have provided an unprecedented opportunity to understand individual, population and community level interactions. In this study, close-range contact rates within a medium-density badger (*Meles meles*) population were investigated using proximity collars. Data were available from 15 badgers, across five different social groups with 12,969 interactions recorded. All collared badgers within social groups contacted each other, with mean intra-group contact frequency 7.75 ± 0.16 contacts/day and mean intra-group contact duration 413.70 ± 16.45 s/day. Inter-group contacts between badgers only occurred between directly adjacent social groups, at a low frequency (<1% of all contacts). Badger intra-group contacts occurred during every hour of the day and had a bimodal distribution pattern that peaked during early morning and evening. There was significant variation in contact frequency according to individual badger, month, sex and social group, independent of age and minimum daily temperature. Mean social group contact rates were not correlated with estimates of social group size. This study contributes to the growing evidence base for significant individual behaviour components within badger social group dynamics, which has implications not only for the transmission of diseases such as bovine tuberculosis but also in terms of the evolution of sociality itself within this species.

Introduction

Animal species interact with each other directly through physical contact or indirectly through various means such as olfaction, vocalisation or behavioural response. These interactions form the basis of the existence of social structures and organisation within wildlife populations and can vary extensively in relation to a range of extrinsic and intrinsic factors in the natural environment (Marsh et al., 2011). In mammal populations, the plasticity of animal interactions occurs across a gradient that ranges from solitary systems to highly complex sociality that are the product of ecological, phylogenetic, developmental and genetic constraints (Kappeler et al., 2013). Many interactions between species are of applied interest to science but of principal interest are those of human health or commercial concern, particularly those associated with zoonotic disease (Bharti et al., 2003) or that have an impact on domesticated species (Pattnaik et al., 2012).

The European badger (*Meles meles*) is a widespread medium-size carnivore that exhibits generally atypical behaviour in Ireland and Britain, with reference to conspecifics in the rest of the species geographic range, in that badgers live in groups and are social (Kruuk, 1978; O'Corry-Crowe et al., 1993). Social group size in badgers can be hyper-variable, even over relatively small spatial scales (Feore and Montgomery, 1999; Tuyttens et al., 2001) with group size a function of ecological and environmental conditions (Johnson et al., 2002; Virgós et al., 2011). Interactions between free-roaming badgers at pasture have been studied over recent decades using a variety of techniques, with the primary aim being to understand the species role in the epidemiology of bovine tuberculosis (bTB) transmission to cattle. Initial studies used direct observation and enclosure experiments (Benham, 1985; Benham and Broom, 1989) to determine interaction rates. More recently, radio-tracking techniques, global positioning system (GPS) collars and proximity collars have been used to quantify interactions between badgers, and badgers with other species (Böhm et al., 2008; Böhm et al., 2009; Mullen et al., 2013; Weber et al., 2013). The application of technology such as proximity collars to wildlife populations has the potential to provide a hitherto unprecedented level of detail in terms of the quantification of animal interactions and how individual behavioural responses to disease dynamics may occur within populations. To-date proximity collars or tags have been deployed on brushtail possums, *Trichosurus cunninghami* (Banks et al., 2011), Tasmanian devils, *Sarcophilus harrisii* (Hamede et al., 2009), racoons, *Procyon lotor* (Prange et al., 2011; Hirsch et al.,

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2013), ungulates (Vander Wal et al., 2013), rabbits, *Oryctolagus cuniculus* (Marsh et al., 2011), badgers and cattle (Böhm et al., 2009; Boyland et al., 2013; Drewe et al., 2013), island fox, *Urocyon littoralis* (Ralls et al., 2013), wire-tailed manakin, *Pipra filicauda* (Ryder et al., 2012), Galápagos sea lions, *Zalophus wollebaeki* (Meise et al., 2013) and have also been used at lion kill sites (Tambling and Belton, 2009). Common to the majority of the studies undertaken has been a high level of individual heterogeneity in contact rates and social networks (e.g. Hamede et al., 2009; Marsh et al., 2011; Drewe et al., 2013).

For badgers, simultaneous close range radio-tracking has shown that within social group contact patterns vary depending on the type of sett used most frequently (Böhm et al., 2008), which may be related to individual disease status (Weber et al., 2012) and other factors such as social status where disease may not be present in the population. Badgers have also been found to have individual variation in contact rates within groups (Böhm et al., 2009) and intricate behaviours in terms of the isolation of bTB positive badgers from their own social group, with potential consequences for disease dynamics at a population level through increased contacts with other badger groups (Weber et al., 2013). Measuring the complexities of individual animal contact behaviour in a multi-host disease system should be seen as a priority in terms of informing disease management and eradication strategies.

In this study, variation in contact rates between badgers in a medium-density population was investigated. It was hypothesised that badger contact patterns in this study population would vary according to social group and at the individual level, with comparatively low-level inter-group contact rates. The results were considered within the context of badger social behaviour and any potential implications in terms of disease epidemiology.

Material and methods

Study area and proximity collars

The study took place in 1,350 ha of a pasture dominated agricultural landscape in Northern Ireland (54°18′N, 5°38′W). This study was part of a larger intensive project on badger ecology, interactions with cattle and badger farmyard intrusion rates (see O'Mahony, 2014a; O'Mahony, 2014b; O'Mahony, 2015a; O'Mahony, 2015b). For the purposes of the current study, data from 5 social groups where at least two proximity collars (see below) were deployed on badgers and had ≥21 contacts are presented. Using a combination of sett surveys, bait-marking and GPS collars it was determined that there were 15 badger social groups (based on each group having a main sett) in the study area, with an estimated overall mean badger density of 3.62 per km^2 (including cubs; 95% CI 2.09–6.09) based on mark-recapture analysis of 2012 live-trapping data using Chapman's (1951) modified Lincoln-Peterson estimator (see O'Mahony, 2014a). The study area was dominated by beef farming enterprises, although some dairy farms also operated and had a regionally high incidence of bTB in cattle (8.03% herd prevalence in 2014; DARD, 2015).

Proximity collars (Sirtrack, Havelock, NZ) were used to investigate contact rates between badgers in the study area. Proximity collars were fitted to badgers through live-trapping licensed by the Northern Ireland Environment Agency. Trapping occurred during August/September 2012, December 2012 and May/June 2013 using peanut baited cage traps. Badger proximity collars deployed in August/September 2012 were retrieved and replaced during live-trapping in December 2012 and retrieved only during May and June 2013. Badgers were anaesthetised using a combination of Vetalar (ketamine hydrochloride; Pfizer Ltd) and Domitor (medetomidine hydrochloride; Orion), sexed, aged, weighed, microchipped and a blood sample taken. Collars weighed ≤2% of animal body weight. Collars were returned from 15 badgers in five different social groups (Table 1) of which two (13.3%) tested positive to bTB using the BrockTB Stat-Pak® test (Chembio Diagnostic Systems, New York, USA), clustered in a single social group (social group B2; collar ID 6 and 7; see Table 1). bTB prevalence in badgers may have been underestimated due to poor sensitivity in the BrockTB Stat-Pak® test (Chambers et al., 2008). It was estimated that 54% (15 of 28) of badgers present in setts were collared in terms of minimum numbers of badgers captured per social group. During live-trapping no individual dispersal or movement between setts in the study area were recorded, as indicated by captures of a badger at a different sett/social group. This was not unexpected given the short temporal period and relatively small spatial scale of the study. A pilot study occurred prior to deployment of collars to determine the settings required to record close range (≤3 m) interactions, which were likely to approximate distance thresholds for direct aerosol transmission of bTB (see Sauter and Morris, 1995; Drewe et al., 2013). Separation time between contacts was set at 15 s.

Badger live-trapping, handling and anaesthesia complied with all relevant laws in the UK on the care and use of animals in scientific research. The research was carried out in accordance with project and personal licences issued by the Home Office UK under the terms of the Animals (Scientific Procedures) Act 1986, and amendments thereof. All procedures were approved by the Agri-Food and Biosciences Institute, Veterinary Sciences Division Ethical Review Panel. This research was part of a larger study on interactions between cattle and badgers in the transmission of bovine tuberculosis (bTB) within the study area that involved using proximity collars to determine close range (≤2 m) contact rates between cattle and badgers. Data were available from 58 cattle and 11 badgers, across several different herds and social groups, between July–December 2012 (see O'Mahony, 2014a). The study determined 376,152 contacts recorded amongst collared animals, however, none were interspecific.

Statistical analyses

Interaction data were downloaded from returned collars. Following recommended procedures, data were amalgamated into 1-min periods when they involved the same pair of collars using Rv.3.0.1 (R Development Core Team, 2013) and any remaining 1-s records post-amalgamation were deleted from the dataset following Drewe et al. (2013). Additionally, contact data from the 24 h period after collar deployment and during trapping periods were excluded from analyses, which effectively excluded summer months. These procedures reduced the quantity of interaction data available (n = 12,969 contacts) but increased data accuracy.

Contact measures were constructed using interaction data to determine the mean daily contact frequency (C_{freq}) and mean daily contact duration (C_{dur}) in s, for each collared animal, based on the total number of contacts and total contact duration, respectively, divided by the total number of days each collar was attached to an animal (Böhm et al., 2009; Marsh et al., 2011). To provide data on mean daily contact frequency and contact duration for specific individual badgers with any other collared animal, the number of individuals collared in each social group was included as a fixed covariate in all subsequent analyses. Therefore, C_{freq} and C_{dur} corresponded to the mean daily contact frequency and duration for specific individual badgers with any other collared animal. These procedures standardised contact measures for badgers. Contact data were analysed at the intra-group level only. Both contact metrics were highly correlated (r = 0.60, n = 1673, P < 0.001) and therefore, only C_{freq} were used in statistical analyses as results were similar for C_{dur}, for which summary data only are presented. Linear mixed model analyses for C_{dur} and full model output for both

Table 1
Summary of the sex, age and number of proximity collars deployed on badgers during the study and contact metrics recorded across five different social groups.

Social group	Collar ID	Sex	Age	No. of days with collar	Total no. of interactions recorded	Mean daily C_{freq} (±SE)	Mean daily C_{dur} (±SE)
B1	1	M	J	74	733	9.91 ± 0.72	339.86 ± 44.34
	2	M	J	81	684	8.44 ± 0.58	222.65 ± 33.19
	3	F	A	176	1509	8.57 ± 0.68	265.18 ± 38.19
	4	M	J	193	1152	5.96 ± 0.38	248.94 ± 27.62
	5	F	A	148	1170	7.91 ± 0.53	278.66 ± 50.73
					5248	7.78 ± 0.27	266.57 ± 18.09
B2	6	F	A	69	537	7.78 ± 0.58	698.89 ± 110.23
	7	F	A	97	754	7.77 ± 0.55	756.38 ± 103.81
					1291	7.77 ± 0.40	732.48 ± 75.89
B3	8	M	A	62	370	5.96 ± 0.53	131.11 ± 25.08
	9	M	A	66	354	5.36 ± 0.44	125.80 ± 24.72
					724	5.65 ± 0.34	128.37 ± 17.54
B4	10	M	A	208	1829	8.79 ± 0.53	687.30 ± 57.54
	11	M	J	59	662	11.22 ± 1.23	562.44 ± 91.69
					2491	9.33 ± 0.49	659.71 ± 49.22
B5	12	F	A	147	1042	7.08 ± 0.49	533.95 ± 64.18
	13	F	A	152	1107	7.28 ± 0.54	412.09 ± 54.39
	14	F	J	71	685	9.64 ± 0.78	533.83 ± 90.53
	15	F	J	70	381	5.44 ± 0.58	282.40 ± 56.06
					3215	7.33 ± 0.29	451.80 ± 33.44
Total/means ± SE				1673	12969	7.75 ± 0.16	413.70 ± 16.45

M, male; F, female; J, juvenile; A, adult; SE, the standard error; C_{freq}, contact frequency; C_{dur}, contact duration (s).

contact metrics are presented in Supplementary material (Table S1).

General linear models (GLM) were used to test for differences in C_{freq} (response variable) according to individual badger collar (fixed factor) with a Poisson distribution and log link function. Generalized linear mixed models (GLMMs) (Genstat 14.0, VSN International, UK) were applied to test for variation in C_{freq} (response variate) with a Poisson distribution and log link function. Fixed factors included were month, social group, sex, age class, and minimum daily temperature (°C). Individual collar ID was included as a random effect in all models. Dispersion parameters were estimated for each model to account for potential over-dispersion. Significance testing used Wald tests for fixed factors and inference on the direction of effects using t tests accepted at $P < 0.05$. To consider if variation in social group contact rates were related to estimates of social group size, the minimum number of badgers captured at each sett during two live-trapping sessions in 2012 were correlated (Spearman rank) with mean group contact rate. Contact patterns over the 24 h period were calculated using combined data across social groups and individuals using 1-min period amalgamated contact data (n = 12,969 contacts) as the cumulative of all contacts that occurred within each hourly interval over the study duration.

Results

Inter- and intra-group badger contact rates

Inter-group interactions between badgers were too few (n = 45/0.35% of contacts) for formal analysis. Inter-group badger contacts occurred between neighbouring badger social groups only, although not with all possible combinations of contiguous social groups (Fig. 1). Only badgers in directly adjoining social groups made inter-group contacts. All badgers within groups contacted each other at least once, with mean intra-group C_{freq} 7.75 ± 0.16 contacts/day (min. 1–max. 49), and mean intra-group C_{dur} 413.70 ± 16.45 s/day (min. 2–max. 5339). There was considerable variation in mean daily C_{freq} between social groups, ranging from 5.65 to 9.33 contacts per day, and mean daily C_{dur} ranging from 266.57 to 732.48 s per day (Table 1). Mean social group contact rates were not correlated with estimates of social group size ($r_s = 0.31$, $n = 5$, $P > 0.60$).

Variation in intra-group badger contact rates

There were significant differences between individual collared badgers mean daily C_{freq} (GLM: $F_{14} = 6.42$, $P < 0.001$). Contacts between badgers occurred during every hour of the day and combined data across social groups and individuals indicated a bimodal pattern of intra-group contacts, with peaks from 06:00 to 07:00 h and 18:00 to 19:00 h (Fig. 2). Month, social group and sex had a significant effect on C_{freq} (GLMM: $F_{8,1422} = 33.93$, $P < 0.001$; GLMM: $F_{4,5} = 27.82$, $P < 0.005$; GLMM: $F_{1,3.8} = 12.62$, $P < 0.05$; respectively; see Fig. 2 and Table 1). Badger C_{freq} were lowest in February–May (Fig. 3) and for male badgers, and were greatest in social group B4. Animal age and daily minimum temperature had no effect on C_{freq} (GLMM: $F_{1,6.3} = 1.22$, $P = 0.309$; GLMM: $F_{1,1652} = 0.33$, $P = 0.568$; respectively). Significant effects of month, social group and daily minimum temperature were found in relation to C_{dur} (see Table S1, supplementary material).

Discussion

Badger contact rates

Decades of research into badger ecology, behaviour and social organisation using 'traditional' techniques such as bait marking, mark-recapture and radio-tracking have provided us with a fundamental knowledge of badger behavioural ecology and these techniques will continue to increase our knowledge of this species. Building on this strong base, recent technological breakthroughs and analytical achievement that include whole genome sequencing (Biek et al., 2012), proximity collars (Böhm et al., 2009; Weber et al., 2013; this study), GPS collar deployment (MacWhite et al., 2013), stable isotope analysis (Robertson et al., 2014) and magneto-inductive tracking (Noonan et al., 2015) are opening important additional research capabilities and opportunities.

In the current study, contact metrics revealed that all badgers interacted to some extent within social groups whilst between social group contacts were negligible but sufficient to ensure

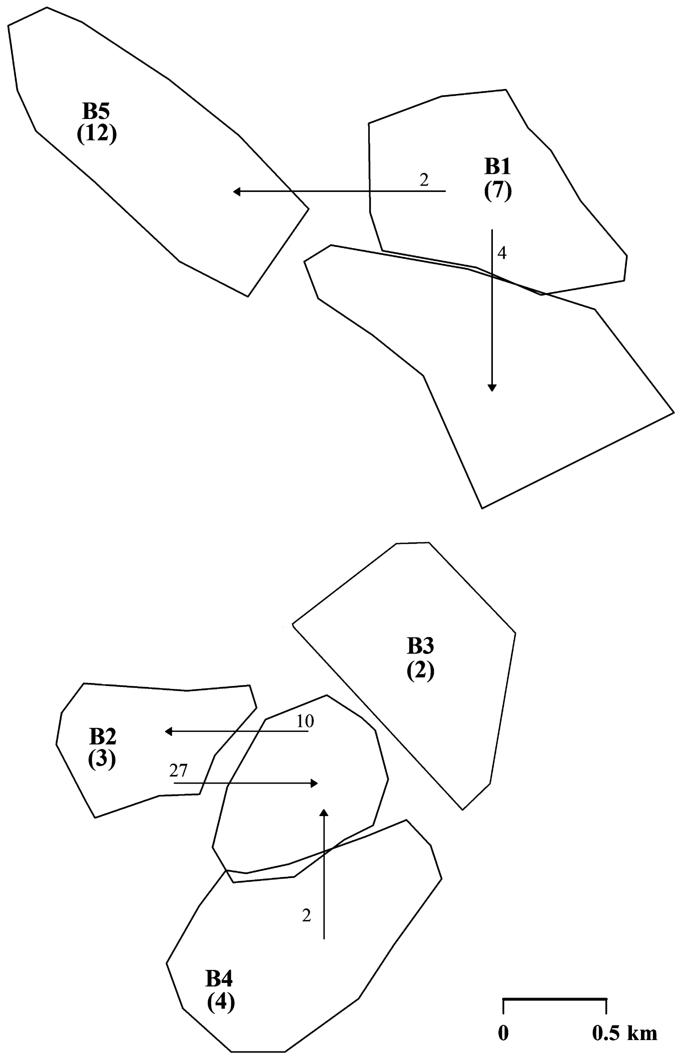

Fig. 1. Illustrated intergroup badger contact patterns determined from proximity collars. Social group (see Table 1) denoted by **B** within territory (polygon); number in parentheses represents minimum number of badgers (incl. juveniles) in social group from live-trapping; arrow and associated number indicates direction and frequency of contact. Unlabelled social group territory (polygon) had total number of contacts ≤20 and/or only a single badger collared, which were not included in further analyses.

population connectivity. There was also variation in contact rate frequency according to individual badger, social group, sex and temporal period, at both month and hourly intervals, independent of animal age and minimum daily temperature. Badger contact patterns conformed to study hypotheses in terms of variation at social group and individual level, with comparatively little inter-group contacts. Badgers within the study population interacted, on average, approximately eight times daily for an approximate total time of 53 min per day. In terms of daily contact duration (see supplementary material), in addition to month and social group, minimum daily temperature also had significant effects. Daily badger contact duration was negatively related to temperature indicating that animals were in contact for longer during periods of low temperature and less during periods of high temperature. Although the temperature variations in the current area were not extreme (range 2–19 °C), badgers would have benefited from thermoregulatory gains through prolonged contact during periods of low temperature. In raccoon populations, Robert et al. (2013) found similar results in that contact duration was significantly greater during cold weather periods, with thermoregulatory benefits to the species.

In terms of badger ecology these results are generally corroborated in the literature. For instance, although badgers are a polygynandrous species and multiple mating occurs with individuals from different social groups (Carpenter et al., 2005; Dugdale et al., 2011), the level of close-range contact between badgers from different social groups can be small (Böhm et al., 2008; this study), although contact rates may vary with population density (see Macdonald et al., 2008). Overall contact rates followed a bimodal pattern with peaks during the early morning and late evening, which corresponded to grooming and play behaviour outside setts during animal emergence and return (Fell et al., 2006). Badger contact rates were greatest in autumn and least during winter and were lowest between February and April, although data from all seasons (i.e. summer) were not available. In terms of badger ecology these periods are important from an ecological and reproductive perspective. During winter badgers are less active, particularly during cold periods (Goszczynski et al., 2005), and contact rates may be lower after birth and during weaning (i.e. February to April, incl.). Higher contact rates during autumn months could reflect increased periods of activity or social interaction outside setts corresponding to a secondary peak in badger territorial delineation (Delahay et al., 2000). Fewer contacts were recorded on male badger collars, particularly during late autumn and winter months in the current study. Movement between social groups can be higher during these periods, particularly for male badgers (Macdonald et al., 2008). Therefore, reduced contacts by males could have been related to inter-group movements increasing the likelihood of contact with non-collared badgers and decreasing opportunities for contact within natal social groups.

Implications for disease epidemiology

This study monitored close range contact between badgers and found significant heterogeneity in contact rates according to a range of factors. If bTB transmission is influenced by variation in contact rates and conditions are suitable for the infection to be transferred, then the current study suggests that badgers may be more susceptible to bTB infection during certain seasons (i.e. autumn). Intuitively bTB may also transmit more frequently in setts where contact rates are higher, which may be related to individual badger behaviour. bTB transmission directly between badgers can be via aerosol inhalation of bacilli of *M. bovis* (Nolan and Wilesmith, 1994) and/or bite wounds (Corner, 2006), with the risk of transmission influenced by the number of infected individuals, and their infectious status, within a population and the number of susceptible animals available to be infected (Corner, 2006). Indirect transmission of bTB can be potentially facilitated through interactions at various fomite sites including farmyards (Garnett et al., 2002; Ward et al., 2008; Tolhurst et al., 2009; O'Mahony, 2015a; O'Mahony, 2015b), water troughs (Ward et al., 2008; O'Mahony, 2014b) and latrines (Drewe et al., 2013).

The results of the current study may have implications for disease modelling and the epidemiology of diseases such as bTB within badger populations. Few studies have published data on badger contact rates using proximity collars (Böhm et al., 2009; Weber et al., 2013; this study). The current study took place in a medium to high-density population in the Irish context (Sleeman et al., 2009; Byrne et al., 2012; Byrne et al., 2014a) but substantially lower than parts of southwest England. In the current study there were lower contact frequencies and duration between badgers than previous studies in England, even though collars operated at similar contact distance tolerances (Böhm et al., 2009). Additionally, contact rates in different social groups were not related to estimates of social group size but the sample size of groups available was small. The prevalence of bTB can be higher in smaller social groups (Woodroffe et al., 2009) and models of disease transmission cannot

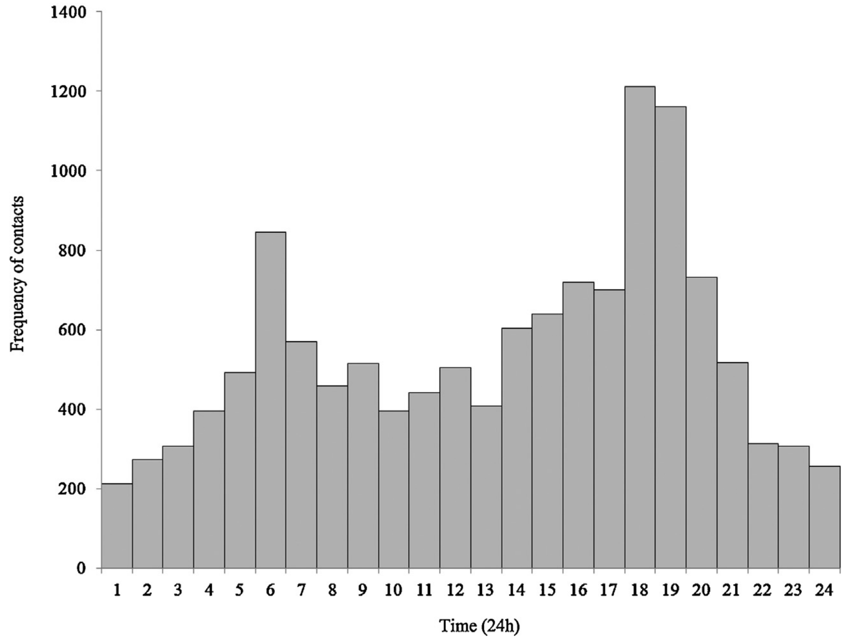

Fig. 2. Cumulative contact frequency (C_{freq}), by hour, for all badgers with proximity collars during the study.

parameterise potential contact rate variation with group size because such data is not available (Hardstaff et al., 2013). Given the relatively few studies available on badger interactions and contact rates, further quantitative research is required involving individuals across a range of densities, social group sizes and habitats to elucidate underlying mechanisms and inform the development of disease transmission models.

Use of proximity collars

An intriguing and potentially novel finding in the current study was that contacts occurred between at least two badgers during every hour of the day. Badgers are typically active at night and can spend considerable amounts of time interacting at dawn and dusk close to their setts. The number of interactions recorded during daylight hours (09:00–17:00 h; 38.1% of all interactions) suggest that collars recorded contacts when badgers were in their setts. Close and prolonged contact between individuals in setts would be expected to facilitate bTB transmission (Weber et al., 2012). However, the capability and distance tolerance to which proximity collars were able to record contacts whilst underground was not explicitly tested in the current study and no details are available in the literature. It is likely that tolerance settings from field trials above ground or in laboratory situations would not be relevant to the internal structure of badger setts that often consist of long tunnels, combined with chambers where the UHF signal could be deflected and reflected. Until the performance of proximity collars have been tested in badger setts, it is not possible to comment on whether or not observed contact rates accurately reflected badger behaviour within setts or interference with UHF signals, but it

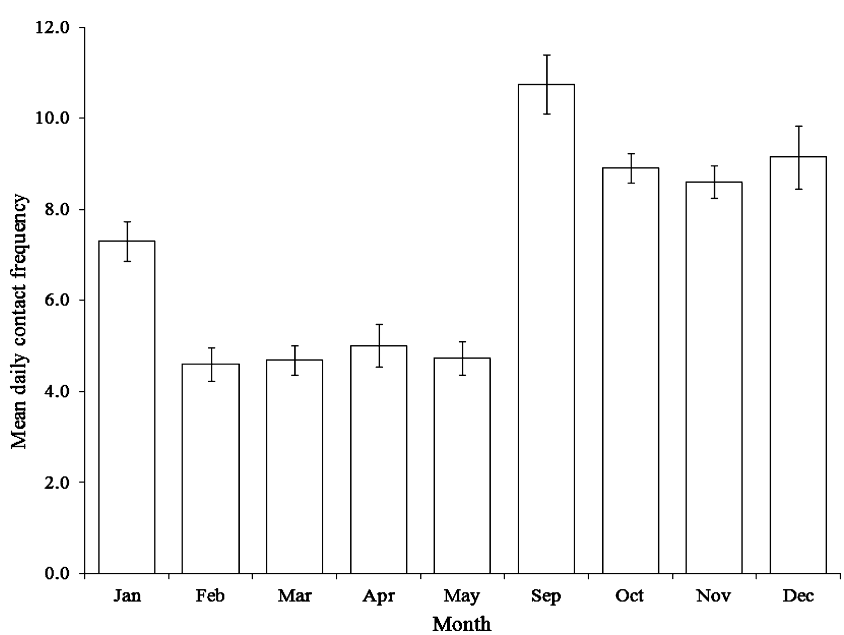

Fig. 3. Mean daily contact frequency (C_{freq}) ± SE during each month between badgers fitted with proximity collars.

is an interesting potential worthy of further consideration. Other new technology such as magneto-inductive tracking may be more applicable to subterranean monitoring of badger ecology (Noonan et al., 2015).

Proximity collars are a relatively new technology and whilst offering exciting potential in determining a range of ecological and behavioural traits in wildlife populations, they have acknowledged limitations. These include reliability issues in determining the true frequency and duration of contacts (Drewe et al., 2012), collection of large quantities of redundant data at the edge of detection range (Prange et al., 2006), reduced distance detection tolerance over time (Drewe et al., 2012), individual collar variation in contact data logging performance (Boyland et al., 2013), poor reciprocal agreement between collars (Watson-Haigh et al., 2012) and collar data provides no contextual information concerning animal contacts (Krause et al., 2013). Yet studies that have compared the performance of proximity collars versus various other contact assessment methods have indicated that proximity collars can provide useful and reliable contact data (see Walrath et al., 2011; Meise et al., 2013; Lavelle et al., 2014). As with all collar types a fundamental issue relates to the sample size of individuals collared and obtaining a sufficiently large number to infer patterns across populations. For instance, determining long distance dispersal attempts by badgers using tracking collars can be hampered by small sample size and study area scale, relative to using more traditional techniques such as mark-recapture (see Byrne et al., 2014b).

In conclusion, this study deployed proximity collars in a medium-density badger population, providing unique data from an Irish population that is comparable to that from other jurisdictions. The study has provided an important insight into interactions between free-living badgers in the rural environment. A fundamental output from the study is the importance of heterogeneity in interaction patterns within this population of badgers, operating at an individual, social group and temporal level. Whilst badgers in Ireland and Britain are a gregarious species, inherently, social groups consist of individuals that vary in their trappability (Tuyttens et al., 1999; Byrne et al., 2012), foraging niche (Robertson et al., 2014), spatial ecology (MacWhite et al., 2013), dispersal (Macdonald et al., 2008; Byrne et al., 2014b), den maintenance provision (Stewart et al., 1999), contact rates (Böhm et al., 2009) and potentially their activity in farmyards (O'Mahony, 2015b). The importance of the individual in shaping the formation, stability and extension of social groups, and in the epidemiology of diseases within group forming species such as badgers is an increasingly important research area in all aspects of ecological, behavioural and epidemiological research.

Conflict of interest

The author declares that there is no conflict of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2015.07.002.

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