

An Active-Radio-Frequency-Identification system capable of identifying co-locations and social-structure: validation with a wild free-ranging animal

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ABSTRACT

1. Behavioural events that are important for understanding sociobiology and movement ecology are often rare, transient and localised, but can occur at spatially distant sites e.g. territorial incursions and co-locating individuals. Existing animal tracking technologies, capable of detecting such events, are limited by one or more of: battery life; data resolution; location accuracy; data security; ability to co-locate individuals both spatially and temporally. Technology that at least partly resolves these limitations would be advantageous. European badgers (*Meles meles L.*), present a challenging test-bed, with extra-group paternity (apparent from genotyping) contradicting established views on rigid group territoriality with little social-group mixing.
2. In a proof of concept study we assess the utility of a fully automated Active-Radio-Frequency-Identification (aRFID) system combining badger-borne aRFID-tags with static, wirelessly-networked, aRFID-detector base-stations to record badger co-locations at setts (burrows) and near notional border latrines. We summarise the time badgers spent co-locating within and between social-groups, applying network analysis to provide evidence of co-location based community structure, at both these scales.
3. The aRFID system co-located animals within 31.5 m (adjustable) of base-stations. Efficient radio transmission between aRFIDs and base-stations enables a 20 g tag to last for 2-5 years (depending on transmission interval). Data security was high (data stored off tag), with remote access capability. Badgers spent most co-location time with members of their own social-groups at setts; remaining co-location time was divided evenly between intra- and inter-social-group co-locations near latrines and inter-social-group co-locations at setts.

Network analysis showed that 20-100% of tracked badgers engaged in inter-social-group mixing per week, with evidence of trans-border super-groups, i.e., badgers frequently transgressed notional territorial borders.

4. aRFID occupies a distinct niche amongst established tracking technologies. We validated the utility of aRFID to identify co-locations, social-structure and inter-group mixing within a wild badger population, leading us to refute the conventional view that badgers (social-groups) are territorial and to question management strategies, for controlling bovine TB, based on this model.

Ultimately aRFID proved a versatile system capable of identifying social-structure at the landscape scale, operating for years and suitable for use with a range of species.

Key words: European badger, co-location, *Meles meles*, network analysis, RFID, social-group, sociobiology, territory, tracking, wildlife management.

INTRODUCTION

Locating animals relative to one another (co-location) is fundamental to understanding sociobiology, gene-flow, dispersal patterns, and disease epidemiology, *inter alia* (Hansson 1991; Kappeler *et al.* 2013; Woodroffe *et al.* 2016), because co-location provides opportunities for animals to interact directly or indirectly. Such insights are also essential to designing effective wildlife management strategies (Carter *et al.* 2007; Woodroffe *et al.* 2016).

Conventional reliance on observation, or coarse-scale tracking technologies, can lead to misinterpretation of animal societies, especially when the study species is rare, elusive, cryptic and/or nocturnal, and thus less amenable to surveillance (Wilson & Delahay 2001). These issues are compounded further in high-density populations and in social-systems involving hierarchies. In such circumstances, monitoring the activities of a sufficient number of individuals, or diversity of socio-types is essential, because focusing on individuals that are prominent in society, or easily detectable/trappable, generates interpretive bias (e.g. Tinnesand *et al.* 2015).

That social organisation is often misconstrued is increasingly exposed by genetic pedigree, revealing patterns of hitherto unknown extra-pair/group paternity, the breeding contribution of non-territory holding floaters within populations and the extent to which unseen out-breeding maintains gene flow and averts inbreeding depression (e.g. Burke & Bruford 1987; Clutton-brock 1989; Zack & Stutchbury 1992). Important behavioural events may be transient, infrequent and therefore difficult to record without long-term monitoring at high temporal resolution. When the spatial scale of studies is restricted, rare, long distance animal movements (affording

opportunities for landscape scale gene flow and disease spread) can go unobserved (Byrne *et al.* 2014).

These deficiencies have, in part, arisen through technological limitations, where (near) continuous and simultaneous tracking of two or more individuals is necessary to identify dynamic interactions (Doncaster 1990). Furthermore, traditional tracking approaches, e.g. visual observation or radiotelemetry, risk perturbing the very behaviour under observation (Böhm *et al.* 2008). Newer, non-tagging methods such as eDNA (environmental DNA; residual DNA from an organism remaining in its environment) and camera trapping (Powell *et al.* In press) may be used to establish presence/absence at specific locations but eDNA cannot locate in time, camera trapping is restricted by field of view and nocturnal illumination, and both are limited by poor longevity (eDNA degrades; camera trap batteries deplete; memory cards fill with non-target triggers).

Tracking technologies are, however, increasingly facilitating higher resolution recording of animal movement patterns (Böhm, Hutchings & White 2009), and referencing of contacts spatially, to infer both with whom and where contacts occur (Woodroffe *et al.* 2016). Monitoring transgressions into neighbouring territories, and co-locations with neighbours at the edge of individual (or group) ranges, could potentially expose population-level connectivity.

Ability to co-locate is particularly important because co-location represents an animal's opportunity to mate, transmit disease (directly or indirectly), or otherwise socially interact, or ignore each other; these opportunities are key, even when co-location behaviour remains unknown. Established technologies, potentially capable of positioning animals (either alone or co-locating) with sufficient defined spatial accuracy to answer sociological questions, include: Very High Frequency radio

tracking (VHF) and the digital equivalent ‘Coded tags’ (e.g. www.Lotek.com); Global Positioning System (GPS tags); Passive Integrated Transponders (PITs); Proximity Tags (VHF, GPS and PIT reviewed by Ellwood, Wilson & Addison (2007), Proximity tag utility reviewed by O'Mahony (2015)). These technologies are animal-borne (usually via collar/harness) with differing functionality that is either advantageous or disadvantageous depending on research goals (Table 1); none can identify behaviour or actual interaction.

Table 1. Comparison of functionality of established tracking technologies and aRFID. References: [1] (Kenward 2001), [2] (Böhm *et al.* 2008), [3] (Kays *et al.* 2011), [4] (Aplin *et al.* 2012), [5] (Böhm, Hutchings & White 2009), [6] (O'Mahony 2015), [7] (Drewe *et al.* 2012), [8] (Woodroffe *et al.* 2016), [9] (Sigrist, Coppin & Hermy 1999).

Function	VHF	Coded	GPS	Proximity	Radio-Frequency-Identification (RFID)	
					Passive (PIT)	Active (aRFID)
Summary	'Radio-tracking' a radio signal emitted by animal-borne tag [1]		Satellite-based tracking by animal-borne tag. Especially suited to inaccessible habitats	Reciprocal transception of radio signals, between tags, logs proximity [5, 6]	Batteryless tags energised remotely, read by static 'Reader'	Tags designed for reliable detection by base-station
Detection range	Adjustable (100-1000+ m). Designed to maximise detection distance.		Absolute location	Adjustable (<1m-10+m)	<10cm	Adjustable (<1m-100+m)
Manual/ Autonomous	Generally manual (risks disturbing study animals [2]); some expensive automated systems [3].		Autonomous. Logs position on pre-programmed schedule.	Autonomous (minimising disturbance)		

Co-location ability	Via triangulation requiring two operators. Fine-scale location unpredictable making co-location unreliable	By chance (relative to pre-determined schedule [8] or randomly)	Designed to co-locate but not referenced spatially unless some tags positioned at fixed points [7]	Relative to fixed resources	
Location accuracy	Unpredictable (<10-100+m)	<5-100+m. May be highly unpredictable depending on habitat [9]	Adjustable (<10cm-1+m; but see [6])	<10cm. Requires animal in close contact with reader [4]	Adjustable (~1m-100+m)
Data security	High. Off tag (recorded manually)	Low. On tag (requires recapture unless combined with data transmission technology, reducing battery life)	High. Off tag (detections logged securely by static, automated 'Readers')		
Active transmission	1-way	None	2-way	None	1-way

If rare or transient events are to be recorded, tags need to be long-lived. Tag longevity is primarily determined by the battery capacity required to: a) make any necessary radio transmissions (one or two-way); and b) perform any necessary on-tag data-processing and storage. Battery capacity depends on battery type, temperature, and species-appropriate battery size, shape and weight. Because VHF and Coded tags are simple one-way transmitters, they are relatively twice as battery efficient as two-way transmitting Proximity tags. With GPS there are no transmission costs, but battery life benefits of this are outweighed by a heavy burden of on-tag data processing, giving GPS shorter longevity than VHF, Coded or PIT tags. Because PIT tags are energised externally they have an almost infinite lifespan, but only a very short detection range. Because of their small size and low weight (<10mm, <1g), PIT tags can often be injected subcutaneously.

While established technologies have various merits and deficits, ability to detect potentially transient, infrequent events, would benefit from an autonomous, continuously active, scalable, system with predictable spatial accuracy, increased tag longevity and high data security.

Here, we establish the functionality of a system that fulfils this niche: aRFID tags coupled with static automated aRFID-detector equipped, wirelessly-networked, base-stations (see Dyo *et al.*'s (2012) technical description, and Table 1 for comparison with established tracking technologies. This technology was adapted from a commercially-available security industry system, designed to protect valuable assets in small, defined areas (tens of metres) with good reliability (e.g. security of National Portrait Gallery exhibits, <http://www.wavetrend.net>).

We validated this aRFID system as an animal co-locating technology, capable of operating for years, via a short 13-week proof of concept study, tracking group-living European badgers (*Meles meles*) in a high-density UK population. Specifically, we investigated whether detailed aRFID data could corroborate established knowledge of the sociobiology of this model species, while providing new insights. Mounting circumstantial evidence suggests hitherto unrealised connectivity between badger groups, refuting the established view that high-density badger populations are rigidly territorial. For instance, our study population (>40 badgers/km²) exhibits 48% extra-group paternity (Annavi *et al.* 2014) and at any trapping session, c.19.8% of individuals are discovered making temporary inter-group visits (Macdonald *et al.* 2008). Nevertheless, high-density badger populations appear sufficiently socially rigid that they confine bovine tuberculosis (*Mycobacterium bovis*; bTB) transmission such that culling-induced perturbation increases inter-group contagion (Macdonald, Woodroffe & Riordan 2015). Elsewhere, in lower density populations (c.1 badger/km²), long distance movements occur both within and between groups: >5km in Spain (Revilla & Palomares 2002); >20km in Ireland (Byrne *et al.* 2014), where bTB may be less constrained by group (Olea-Popelka *et al.* 2005). These observations highlight the sociobiological importance of developing a system that

can detect events at high temporal resolution and is scalable to detect long distance movements.

By recording badger co-locations at a relatively few, important, fixed locations we reveal the extent to which:

- i) badgers not only co-located with members of their own social-group – an ‘easy test’, but also with extra-group members, a ‘hard test’ (because such events may be transient and infrequent, or absent);
- ii) any inter-group co-locations occurred at setts or at ‘notional’ territorial border latrines;
- iii) gender affected co-location patterns.

We also evaluate whether:

- iv) inter-group interactions are agonistic (implying either active (Delahay *et al.* 2006) or passive territorial defence (Stewart, Anderson & Macdonald 1997)).

We then applied network analysis (Krause, Lusseau & James 2009), based on the time badgers spent co-locating at setts and latrines, to identify and validate badger communities algorithmically, and compared these with traditional definitions of social-group territories.

MATERIALS AND METHODS

Badger study system

This technological development was conducted at Wytham Woods, Oxfordshire, UK (51:46:26N; 1:19:19W; Fig.1). The Minimum Number Alive (MNA; Macdonald *et al.* (2009)) at this time was 201 adults and 53 cubs, distributed among 23 putative social-groups. Badger territories were interpreted from biennial bait-marking (Delahay *et al.* 2006) and social-group affiliations derived from cage-trapping records using the formula described by (Macdonald *et al.* 2008).

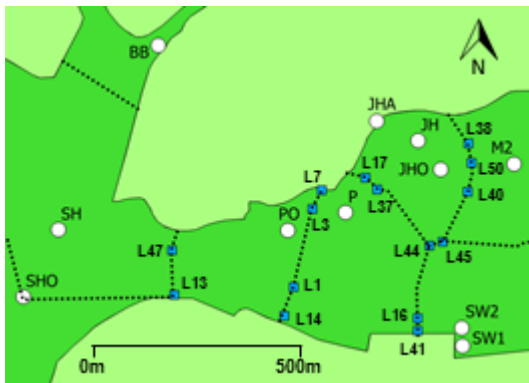


Figure 1. Study area map. Dark-green = wooded; light-green = agricultural land; white circles = sett base-stations (BB, SH, SHO, PO, P, JH, JHA, JHO, M2, SW1&2); blue squares = base-stations at latrines (Ln) shared by two or more social-groups (none found outside woodland); dotted lines are notional woodland territorial borders separating our seven *a priori* defined notional social-groups (SH = SH+SHO; BB; PO; P; JH = JH+JHO+JHA; M2; SW is a dispersed sett requiring two base-stations, SW1 & SW2).

aRFID system and infrastructure

We deployed this system at seven neighbouring social-groups with good historic trapping success and easy access (Fig. 1), over 13 weeks (March-June

2009). Thirty-two adult badgers were trapped and sedated (even sex ratio and numbers per sett targeted), following Macdonald *et al.* (2009), and fitted with Wavetrend, L-series (Wavetrend Ltd), aRFIDs (40x20x3mm; 123mm stainless steel antennas; 3V CR2450 coin cell). aRFIDs transmitted a packet of data every 0.4s for a manufacturer projected 2-year lifespan. Each packet encoded an aRFID's unique identification number plus a serial-counter-number (making individual transmissions identifiable). aRFIDs were hermetically sealed (potted) onto a leather collar in waterproof epoxy resin to protect them from environmental and mechanical damage and allow attachment to badgers. This assembly (the 'aRFID-tag') weighed 80g, roughly 1% of an adult badger's weight (unpotted electronics <20g). aRFID-tags were removed at subsequent trapping events.

Base-stations comprised a Wavetrend aRFID-Reader (detector) integrated with a Tmote-Sky miniature computer (that streamed and processed data received from aRFIDs, storing them in FLASH memory (4Mb)), housed in a waterproof enclosure. Transmissions were received via an external Predator AN400 whip antenna, mounted 2m above ground, connected to the reader via co-axial cable. The Tmote-Sky contained a radio transceiver, capable of exchanging data with other Tmote-Skys (range 125m). A later iteration of this hardware replaced the Tmote-Sky with a Zigbit-AMP and 2Gb SD card, increasing transmission range to 1km and storage capacity to the equivalent of 40 years continuous use (based on average daily data requirements). Data storage and transceiver protocols could be adjusted via the computer's firmware, allowing compression and/or transmission of data summaries rather than total datasets (minimising power and download overheads), as detailed in Dyo *et al.* (2012). The base-station could be powered by anything from a 3V to 12V battery. Importantly, the Zigbit-AMP version increased operational

lifetime from one to ten weeks on a single 12V, 18Ah, battery, or indefinitely if solar-powered. The network of base-stations also included a single solar-powered 'Gateway' with 3G cellular connectivity, adding the capacity to relay data instantaneously to cloud-based storage. For full technical specifications see Dyo *et al.* (2012). Each base-station logged badger presence continuously until the badger was out of detection range (went underground or left the site). These time periods were termed 'Detections'.

We conducted extensive field trials to determine the detection range of aRFIDs: 95% of transmissions were within 31.5m of base-stations (90% within 27.9m; 80% within 22.5m), with a negligible effect of both base-station (including location and associated variation in vegetation density; N=9 site/base-stations) and aRFID-tag (2 old and 2 new tags tested). See Supplementary Information (S1) and Dyo *et al.* (2012).

We placed base-stations at 10 badger setts affiliated with 7 social-groups and at all 15 active shared border latrines conventionally believed to infer group-territory interfaces (established from contemporaneous bait-marking, and in use for ≥ 2 years preceding the study; Fig. 1). No latrines met this definition between the BB social-group and others, so the border shown in Fig. 1 depicts the historic boundary from Macdonald *et al.* (2008).

Data, protocols and analyses

Detections were coded, *post-hoc*, as time intervals, using the 'lubridate()' package (Grolemund & Wickham 2011) in R (R Core Team 2014), and all detection combinations were compared iteratively, per base-station, per night, to identify overlaps in space and time. Dyadic overlaps indicated the 'co-location' of badgers. In

this way we calculated the duration of each co-location, in seconds. Placement of the base-stations was constrained by the location of setts and latrines. In six cases, the detection range of adjacent base-stations overlapped, providing opportunities for co-locations (between dyadic pairs) to be detected by two base-stations at the same time. To compensate for this possibility, we adjusted total co-location durations, for each affected base-station-pair, using a multiplier based on the proportion of range overlap by area (multipliers were L17:L37=0.87; L38:L50=0.94; L44:L45=0.81; SW1:SW2=0.90; L3:L7=0.95; L16:L41=0.79). These adjusted values are reported here.

We fitted a fixed-effects normal-errors GLM model (R `lm()`) to explore the effects of dyadic social-group relationship, site-type, gender dyad, and week, on co-location duration per dyad (Box-Cox transformed to meet assumptions of normal errors and variance). First, co-locations were allocated to different predictor categories for each week (13 levels): 1) gender dyad involved (levels: male-male, male-female, female-female); 2) dyadic social-group relationship (levels: same, different); 3) co-location site-type (levels: sett, latrine). Total co-location time, per category, per week, was divided by the number of gender dyads of each type present in the relevant week, to control for any collar losses occurring, producing the variable 'Co-location duration per dyad'. Weeks were treated as levels of categorical time.

To evaluate active territorial defence via agonistic interaction we examined bite-wounding on badgers caught at the start and end of the study: scarring is visible for at least six months (Chris Newman unpublished data; Macdonald *et al.* 2004).

The 'igraph()' package (Csardi & Nepusz 2006) was used to convert dyadic co-location data into network graphs, per week, using co-location duration as 'Edge'

values (Edges are lines connecting nodes on a network, the thickness of Edges equating here to dyadic strength of association between nodes (badgers)).

Networks were generated separately for co-locations that occurred at (i) setts, (ii) latrines, and (iii) setts and latrines combined (the 'All' network). We applied the 'Fast-Greedy' (F-G) community detection algorithm (Clauset, Newman & Moore 2004) to each network to estimate community structure blindly (resulting groups termed 'Communities'), thus enabling direct comparison with our *a priori* definition of social-group composition based on trapping records.

We fitted fixed-effects normal-errors GLM models (R `lm()`) to explore the effect of site-type (sett or latrine) on: 1) the ratio, per week, of the number of badgers co-locating *within:between* social-groups (log transformed); 2) the proportion of badgers, per week, involved in inter-group co-locations (logit transformed).

RESULTS

System performance

Compared to other technologies (Table 1), aRFID: (i) had a detection range of 31.5m (similar to that to which Proximity tags can be adjusted); (ii) co-located animals relative to fixed resources with a definable range accuracy; (iii) with high data security (data stored off-tag); and (iv) wireless data access. Critically, because signal transmission was one-way, coupled with the pre-defined short transmission range, these aRFID-tags would have a projected lifespan of 2-5 years (depending on transmission interval setting). The only aRFID-tag failures (10 tags) were mechanical, due to broken antennas preventing signal transmission.

Patterns in detections

We recorded 1,834.1 h of detections (n=161,333) over the 13-week study period, during which the number of badgers wearing operational aRFIDs decreased from 32 to 18 (approximately half of ca. 50-60 adults typically resident). Of these detections, 56.1% occurred at setts (males=454.1h (24.8%), females=575.0h (31.3%)) and 43.9% at latrines (males=297.6h (16.2%), females=507.3h (27.7%)). Over 40% (42.8%, 785.1h) of detections involved periods during which animals co-located for part of the time; these parts (co-locations) totalled 291.3 hours.

Patterns in time spent co-locating

There was evidence that the effect of site-type on co-location duration per dyad (from here 'co-location duration') varied with week, and that the effect of dyadic social-group relationship on co-location duration varied with site-type (interaction

terms, Table 2). Inspection of the week:site-type data reveals that the general pattern was for greater co-location durations at setts than latrines but that this was not the case in just two of 13 weeks. Therefore this interaction is unlikely to be biologically significant (Supplementary Fig. S1). The dyadic social-group relationship:site-type interaction is clear in Fig. 2 and was due to badgers from the same social-group being more likely to co-locate at the sett, as would be expected. There were significant main effects of both site-type and dyadic social-group relationship on co-location duration, but none of gender-pair or week (Table 2).

Table 2. ANOVA describing the effect of gender dyad (GD), dyadic social-group relationship (DSGR), site-type (ST) and week on co-location duration per dyad.

	Df	SS	Mean-SS	F-value	p-value
GD	2	0.401	0.200	0.903	0.408
DSGR	1	28.347	28.347	127.829	<0.001
ST	1	12.365	12.365	55.757	<0.001
Week	12	3.515	0.293	1.321	0.216
Week:ST	12	10.102	0.842	3.796	<0.001
DSGR:ST	1	7.621	7.621	34.366	<0.001
Residuals	117	25.946	0.222		

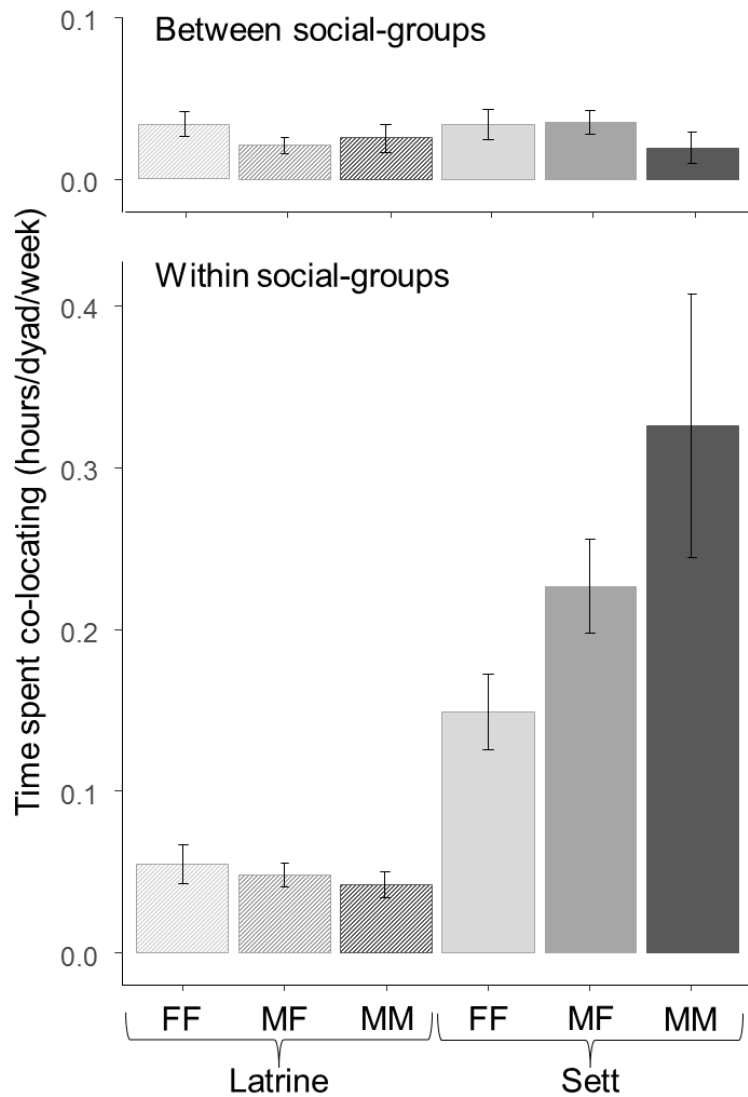


Figure 2. Average time, per dyad, per week, spent co-locating, per combination of gender-dyad group (male-male, female-female, male-female), site-type (sett or latrine), and dyadic social-group relationship (intra-, or inter-social-group).

Having established the main effects of the model, we now emphasise the average effect sizes in detail (Fig. 2). Badgers spent more time co-locating with individuals from the same social-group (0.81 h/dyad/week, se=0.07; 83.9%) than with individuals from different social-groups (0.16 h/dyad/week, se=0.02; 16.1%). Co-

locations between social-groups were similar at setts and latrines; whereas, within the same social-group, more time was inevitably spent co-locating at setts (0.67 h/dyad/week, se=0.08; 68.9%) than at latrines (0.15 h/dyad/week, se=0.02; 15.0%), due to implicit co-residency.

The greatest time spent co-locating within the same social-group, at setts, occurred between males (0.33 h/dyad/week, se=0.08; 32.1%), followed by male-female dyads (0.23 h/dyad/week, se=0.03; 22.3%), with least between females (0.15 h/dyad/week, se=0.02; 14.7%). By contrast, badgers from the same social-group spent significantly less time co-locating at latrines than at setts (below 0.06 h/dyad/week, 5.4%).

Badgers from different social-groups spent similar quantities of time co-locating (also below 0.06 h/dyad/week, 5.4%), regardless of site and gender dyad (Fig. 2). Thus we see a dichotomy between the amounts of time badgers from the same social-group spent co-locating at setts versus all other co-locations. These patterns of association are very evident in the Edge connections (and their thicknesses) depicted in our networks (Fig. 4, also Supporting Figs S2-S13).

Importantly, the overall pattern in Fig. 2 was consistent over time. Consequently, the distribution of co-locations across groups (see Fig. 2), which underlies the networks patterns observed (e.g. Fig. 4), are representative of all weeks (see Figs S2-S13 for remaining 12 weeks of networks), thus enabling us to draw general conclusions across weeks.

Evidence for active territorial defence

No collared badgers acquired fresh bite wounds during the study, indicating that neither intra- nor inter-social-group co-locations resulted in sufficiently agonistic encounters to cause evident injury.

Network Analysis

The ratio of badgers co-locating *within:between* social-groups was consistently higher at setts than at latrines (Fig. 3a; GLM, $F_{(1,24)}=38.1$, $p<0.001$; green vs red edges, Fig. 4), indicating a greater likelihood for inter-group co-locations to occur at latrines than at setts; a distinction that cannot be made on the basis of time spent co-locating alone (Fig. 2). Furthermore, inter-group co-locations were enacted by a substantial proportion of the tracked badgers, rather than by a few highly connected individuals: significantly more individuals were involved at latrines (between 67% and 100% [weeks 13 and 4 respectively]) than at setts (between 20% and 48% [weeks 4 and 1 respectively]) (GLM: $F_{(1,24)}=200.3$, $p<0.001$. Fig. 3b).

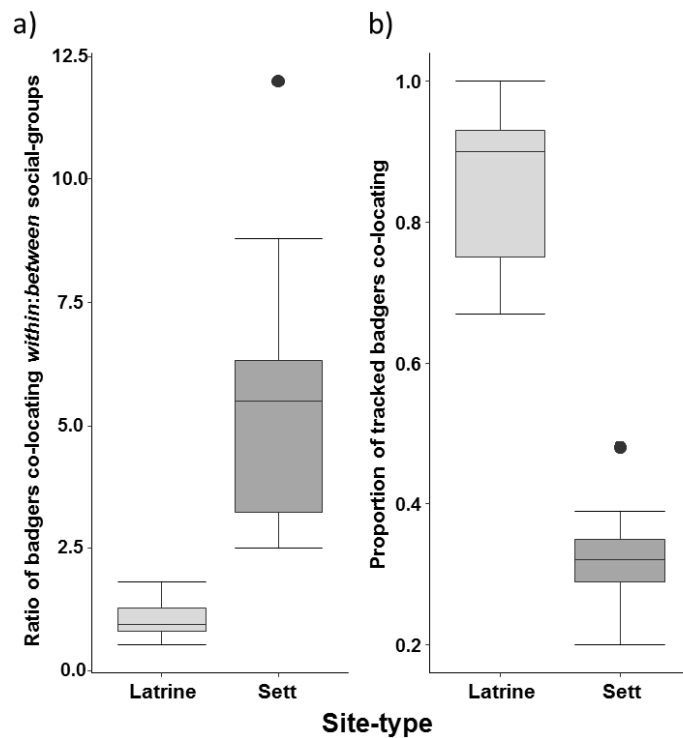


Figure 3. Box-Whisker plots showing co-locations at setts and latrines: a) ratio of badgers co-locating within:between social-groups; b) proportion of badgers co-locating between social-groups.

At setts, aRFID-based community estimates corresponded well with social-group affiliations derived from cage-trapping, validating our network analysis approach (Fig. 4a and Figs S2-S13: compare communities, contained within black lines, with social-groups designated by node colours). There were very few, yet consistent, exceptions (across weeks) where communities included animals from more than one social-group: an individual female residing at social-group M2 associated with one of her JH neighbours in two different weeks; male and female previously trapped regularly at BP were integrated within the SH community.

In contrast, the communities identified by the latrine network were consistently larger and fewer, per week, than those at setts; exposing much greater population

connectivity at latrines. Here, each community comprised a mixture of neighbouring social-groups (Fig. 4b; Figs S2-S13).

Combining setts and latrines in a single network produced a comparable number of similarly composed communities to the communities and social-groups arising at setts alone, but with much greater inter-group connectivity (Fig. 4c).

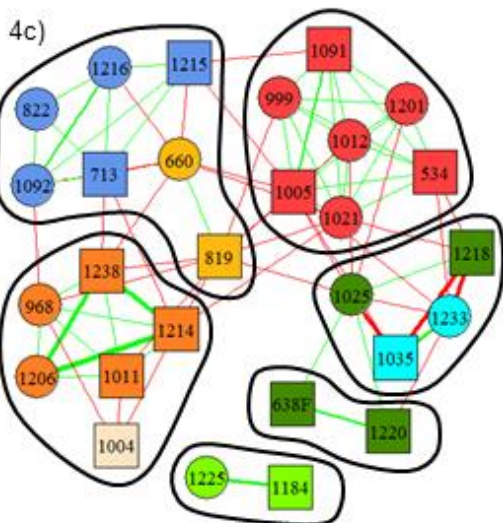
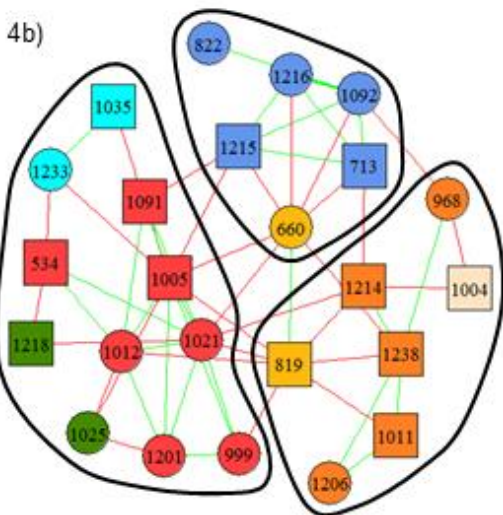
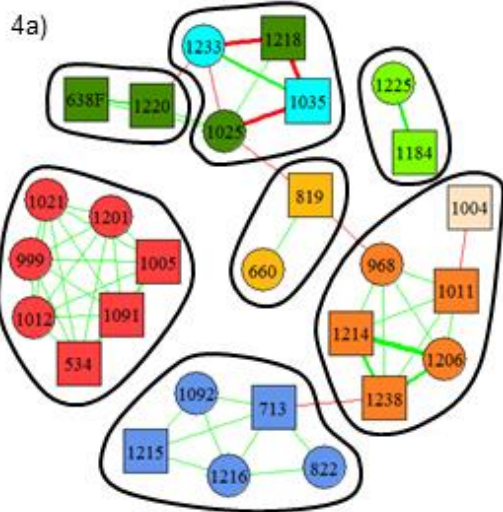


Figure 4. Network patterns from week two co-locations at: a) setts; b) latrines; c) setts and latrines combined ('All'). Node numbers, shapes and colours depict badger IDs, gender (square=female, circle=male), and social-group affiliation from trapping (light-blue=BP, dark-green=SH, light-green=BB, red=PO, gold=P, fawn=M2, orange=JH, dark-blue=W), respectively. Edge thickness is proportional to co-location duration. Edge colour indicates intra- (green) vs inter-social-group (red) co-locations. Black borders indicate network 'community' estimates (from Fast-Greedy algorithm).

DISCUSSION

Our proof of concept study validated the utility of aRFID communicating with autonomous base-stations for studying the sociobiology of a free-ranging wild animal. The system was capable of locating, and therefore co-locating, aRFID-instrumented animals reliably, within a few tens of metres of fixed resources/sites, and able to operate continuously for years. Relative to alternative technologies, this positions aRFID in a distinct tracking niche where tag longevity and the deliberate restriction of detection range enables infrequent and transient events to be detected within small defined areas.

In terms of badger sociobiology, the aRFID system identified social organisation consistent with existing knowledge (Macdonald, Newman & Buesching 2015), but with connectivity at the landscape scale that potentially extended social-group relationships beyond the *status quo*. Similarly, extra-group movements in low(er) density populations have led others to question whether badgers are truly territorial (Revilla & Palomares 2002; Byrne *et al.* 2015). Our observations refute the archetypal territorial defence hypothesis widely proposed for badger social organisation (Kruuk 1978), with implications for the transfer of social and genetic information and disease epidemiology.

System performance

aRFID-tags are specifically engineered in combination with their base-stations (they are not modified long-range transmitters) to: (1) have a short detection range, enabling precise tag location within small defined areas; (2) facilitate lightweight tags, with (3) low power requirements, allowing the system to operate (4)

reliably, and (5) continuously, (6) for many years. These features make aRFID particularly suitable for monitoring animals where they need to be located individually (simple presence/absence) or co-located communally, relative to fixed resources/sites, over long periods of time (years), at multiple sites (scalable to detect long-distance movements).

Such attributes are especially valuable not only for detecting rare, transient and spatially disperse events, such as those providing opportunities for disease transmission and mating, but also where disturbance or site access is restricted and repeated capture/sedation (to download data, swap collars or maintain identification marks) might perturb the population (Böhm *et al.* 2008). Such restrictions rule out non-tagging approaches such as camera trapping (marking required if not naturally patterned), or eDNA (poor temporal resolution; requires frequent site access); see Introduction for further limitations.

Comparison to alternative technologies

Proximity tags are able to record far more co-locations per unit time, than aRFID, because they are not anchored to specific locations; however, our aRFIDs had a five-year maximum lifetime, six times that of the Proximity tag equivalent lasting just nine months (Drewe *et al.* 2012). aRFIDs will theoretically always last at least double the time of Proximity tags (Table 1). aRFIDs will maintain this relative advantage as battery and memory capacity improves across both technologies. Therefore, where co-location is critical, the choice is reduced to deciding which is most important: 1) recording co-location anywhere (but without knowing where), with Proximity tags, or; 2) limiting co-location to fixed resources/sites but for at least

double the deployment time using aRFID; [This second choice might also include PIT tags (with almost infinite tag life) although detection range is a few centimetres].

VHF, Coded and GPS systems are generally not technically suited to co-location (GPS especially is too power hungry to generate locations at the temporal resolution required to co-locate animals for more than a few hours before batteries deplete) although it is possible to gain function by combining technologies. For example, GPS combined with data telemetry systems allows remote data download, while combining GPS with Proximity tags would spatially anchor co-locations. Nevertheless, crucially, enhanced functionality increases power consumption, reducing deployment duration.

Another base-station tracking system, the 'Trace Recorder', transmitted magnetic signals radially (3m range) to be detected by receiver-tags on passing badgers (Kaneko *et al.* 1998). Such a system is capable of generating similar data to aRFID, but for much shorter time periods (3 months) due, as with GPS, to the high energy cost of processing and archiving data on-board a tag.

Future refinements and developments

An important feature of our system was the wireless inter-connectivity of base-stations, potentially giving world-wide access. This allowed modification of our set-up to inform users of data quantities remotely via transmitted summaries, reducing the cost/disturbance of unnecessary visits to download data (remote download of full datasets is energetically inefficient (see Dyo *et al.* 2012). An advantage of transmitted data summaries is that, in the future, experimental design could become dynamic, rather than predetermined, for example, automatically switching on cameras to record transient events when aRFIDs are detected.

Another refinement would be to equip base-stations with directional antennas, giving elongated detection zones suited to monitoring territory borders. Furthermore, our aRFIDs were modified security tags; a bespoke aRFID designed for animals could be reduced by an order of magnitude to weigh 2g, and so be carried by 40g animals (tracking device <5% body weight; Kenward 2001) without reduction of performance (Unpublished data. A. Markham).

System validation: co-location patterns in time

Badgers spent the greatest proportion of time co-locating with individuals from their own social-group (83.9%), predominantly at setts (68.9%); Fig. 2. This ‘easy test’ result was expected, due to co-residency, but important because it demonstrates that aRFID can corroborate known co-location patterns. Had our detection range been too great or small then our easy test would not have been fulfilled (communities resolved too large or too small, respectively), casting doubt on the other patterns observed. Contrary to convention, however, our ‘hard test’ showed that the remaining co-locations (16.1%) occurred between badgers from different social-groups, with visits to neighbouring setts happening within all study weeks (Fig. 4a and Figs S2-S13). This contrasts with just four such events detected over three years using VHF tracking elsewhere (Böhm *et al.* 2008). And, because we instrumented about half of the local resident badger population, and logged data at a relatively few focal sites, these encounters between social-groups represent minima. It is therefore highly probable that, overall, total inter-social-group co-location time was greater, and could reflect levels of connectivity observed in lower density populations (Byrne *et al.* 2014). Furthermore, this pattern was consistent across weeks and unaffected by season, suggesting a stable pattern of inter-social-group

connectivity. High and low density badger populations may therefore exhibit a similar lack of territoriality.

Co-locations by badgers away from the home-sett inferred a deliberate intention to encounter conspecifics, at least by sound and smell, because contacts could easily have been avoided in space and time. This social tolerance was apparent for both intra-and inter-social-group co-locations. At latrines badgers exhibited similar levels of co-location with members of neighbouring social-groups and their own social-group members, irrespective of gender (Fig. 2). This suggests no tolerance bias based on own vs neighbouring group affiliation. This observation was supported by the total absence of bite wounding, where antagonism between neighbours would cause injuries (Macdonald *et al.* 2004).

System validation: network analysis

Network community estimates closely resembled social-group memberships derived from cage-trapping records at setts. For example, the membership of five out of seven social-groups (coloured nodes) were assigned to communities (black outlines) in accord with cage-trapped group affiliations in week 2 (Fig. 4a). Decisively, a single week's co-location data identified communities that took three cage-trapping rounds, spread over five months, to establish (Macdonald *et al.* 2009). We acknowledge, however, that some measure of uncertainty could be informative, for example, placing some badgers as inter-community floaters.

Latrine-based communities were fewer and had more members (Fig. 4b) compared to those at setts (Fig. 3a). This inferred 'Super-groups' at the landscape scale (Evans, Macdonald & Cheeseman 1989), persisting throughout the study. In

combination, these sett and latrine networks (Fig. 4c) revealed far greater connectivity in this population than previously identified by cage-trapping alone (Macdonald *et al.* 2008). Again, this contrasts with the four such events detected over three years by Böhm *et al.* (2008) and with O'Mahony's (2015) finding that <1% of badger Proximity tag contacts involved members of different groups (but note this will at least partly have been a function of a lower population density in these studies, coupled with only very close proximity contacts being recorded, although these still do not infer social interaction).

Network analysis (Fig. 4) revealed yet more inter-social-group connectivity than that based on time spent co-locating alone (Fig. 2), with between 20% and 100% of individuals involved in any given week. Badgers from different social-groups clearly did co-locate occasionally (our hard test) at each other's setts but co-located more frequently around border latrines, albeit for shorter periods of time (compare red lines connecting badgers/nodes in sett and latrine networks, Figs 4a,b and S2-S13). This pervasive inter-social-group connectivity, identified via co-location, clearly provides the opportunity - although, as with other technologies (except cameras), no proof - for actual interaction and further contradicts the traditional view of badger territoriality via active defence (Kruuk 1978). This undermines reliance on bait-marking to determine badger social-structure (Delahay *et al.* 2000). Importantly, this revised picture of badger society also countermands the model used in bTB management scenarios (Carter *et al.* 2007), a contention supported by recent work in Ireland (Byrne *et al.* 2015). Furthermore, recent evidence suggests that badger-to-cattle bTB transmission is rare (Donnelly & Nouvellet 2013) and may at least partly follow an environmental route (Woodroffe *et al.* 2016). Coupled with these observations, our evidence of badger super-groups, through infrequent but regular

co-location, presents a potential opportunity for disease transmission beyond traditional social-group boundaries, regardless of the frequency and mode of infection. We thus recommend aRFID as a versatile system capable of identifying social-structure at the landscape scale.

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AUTHOR CONTRIBUTIONS

Conception/design: SE, DM, CM, NT, CN, AM. Data acquisition: SE, CN, CB, BP, VD, AM. Analysis/interpretation: SE, SB, CN, CB, RM, VN, AM, CM, VL, BP.

Drafting/Revising article: SE, CN, SB, RM, DM, AM. All authors gave final approval and agree to be accountable.

DATA ARCHIVE

Data will be submitted to Dryad.

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Table 1. Comparison of functionality of established tracking technologies and aRFID. References: [1] (Kenward 2001), [2] (Böhm *et al.* 2008), [3] (Kays *et al.* 2011), [4] (Aplin *et al.* 2012), [5] (Böhm, Hutchings & White 2009), [6] (O'Mahony 2015), [7] (Drewe *et al.* 2012), [8] (Woodroffe *et al.* 2016), [9] (Sigrist, Coppin & Hermy 1999).

Function	VHF	Coded	GPS	Proximity	Radio-Frequency-Identification (RFID)	
					Passive (PIT)	Active (aRFID)
Summary	'Radio-tracking' a radio signal emitted by animal-borne tag [1]		Satellite-based tracking by animal-borne tag. Especially suited to inaccessible habitats	Reciprocal transception of radio signals, between tags, logs proximity [5, 6]	Batteryless tags energised remotely, read by static 'Reader'	Tags designed for reliable detection by base-station
Detection range	Adjustable (100-1000+ m). Designed to maximise detection distance.		Absolute location	Adjustable (<1m-10+m)	<10cm	Adjustable (<1m-100+m)
Manual/ Autonomous	Generally manual (risks disturbing study animals [2]); some expensive automated systems [3].		Autonomous. Logs position on pre-programmed schedule.	Autonomous (minimising disturbance)		
Co-location ability	Via triangulation requiring two operators. Fine-scale location unpredictable making co-location unreliable		By chance (relative to pre-determined schedule [8] or randomly)	Designed to co-locate but not referenced spatially unless some tags positioned at fixed points [7]	Relative to fixed resources	
Location accuracy	Unpredictable (<10-100+m)		<5-100+m. May be highly unpredictable depending on habitat [9]	Adjustable (<10cm-1+m; but see [6])	<10cm. Requires animal in close contact with reader [4]	Adjustable (~1m-100+m)
Data security	High. Off tag (recorded manually)		Low. On tag (requires recapture unless combined with data transmission technology, reducing battery life)	High. Off tag (detections logged securely by static, automated 'Readers')		
Active transmission	1-way		None	2-way	None	1-way

Table 2. ANOVA describing the effect of gender dyad (GD), dyadic social-group relationship (DSGR), site-type (ST) and week on co-location duration per dyad.

	Df	SS	Mean-SS	F-value	p-value
GD	2	0.401	0.200	0.903	0.408
DSGR	1	28.347	28.347	127.829	<0.001
ST	1	12.365	12.365	55.757	<0.001
Week	12	3.515	0.293	1.321	0.216
Week:ST	12	10.102	0.842	3.796	<0.001
DSGR:ST	1	7.621	7.621	34.366	<0.001
Residuals	117	25.946	0.222		

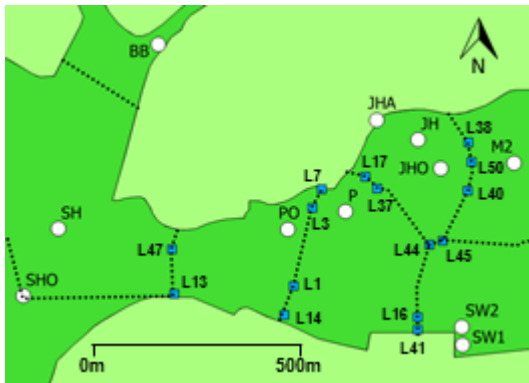


Figure 1. Study area map. Dark-green = wooded; light-green = agricultural land; white circles = sett base-stations (BB, SH, SHO, PO, P, JH, JHA, JHO, M2, SW1&2); blue squares = base-stations at latrines (Ln) shared by two or more social-groups (none found outside woodland); dotted lines are notional woodland territorial borders separating our seven *a priori* defined notional social-groups (SH = SH+SHO; BB; PO; P; JH = JH+JHO+JHA; M2; SW is a dispersed sett requiring two base-stations, SW1 & SW2).

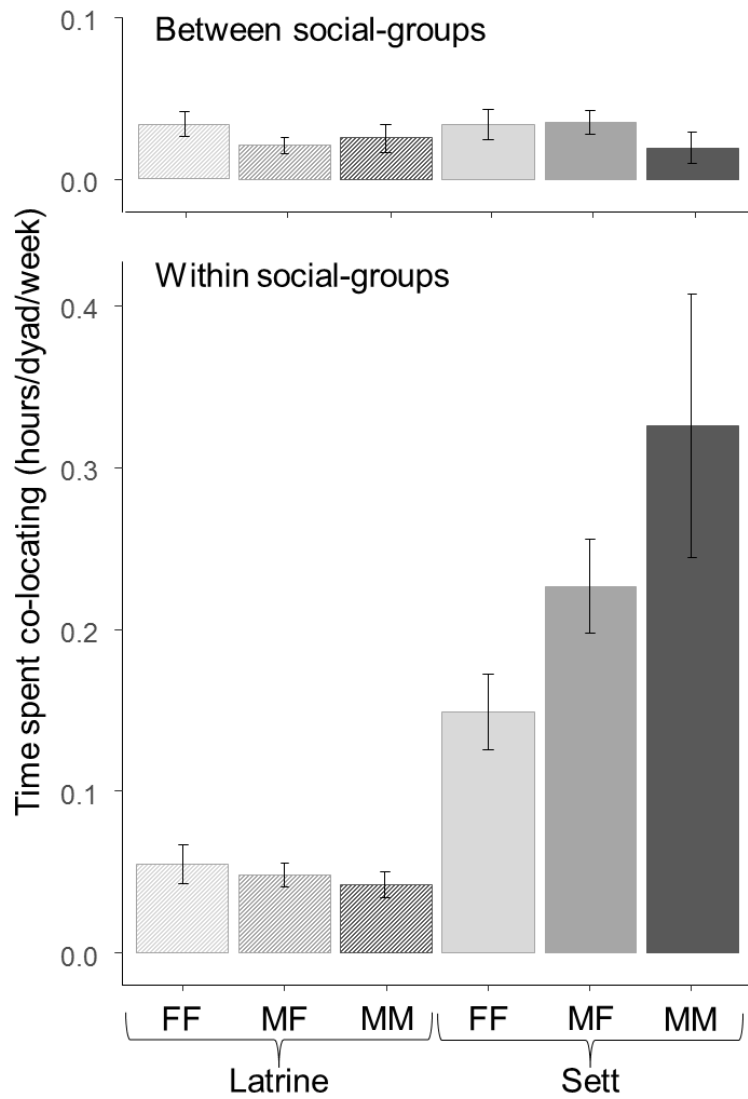


Figure 2. Average time, per dyad, per week, spent co-locating, per combination of gender-dyad group (male-male, female-female, male-female), site-type (sett or latrine), and dyadic social-group relationship (intra-, or inter-social-group).

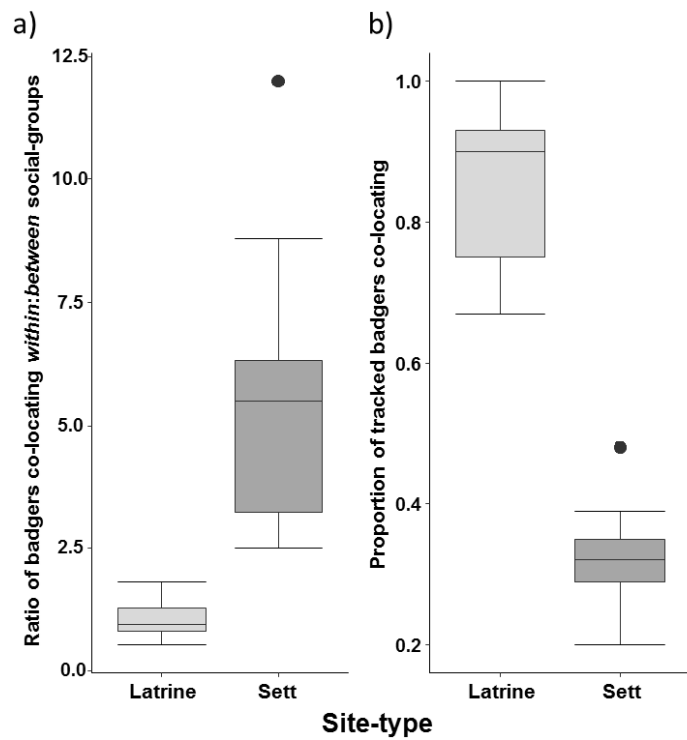


Figure 3. Box-Whisker plots showing co-locations at setts and latrines: a) ratio of badgers co-locating within:between social-groups; b) proportion of badgers co-locating between social-groups.

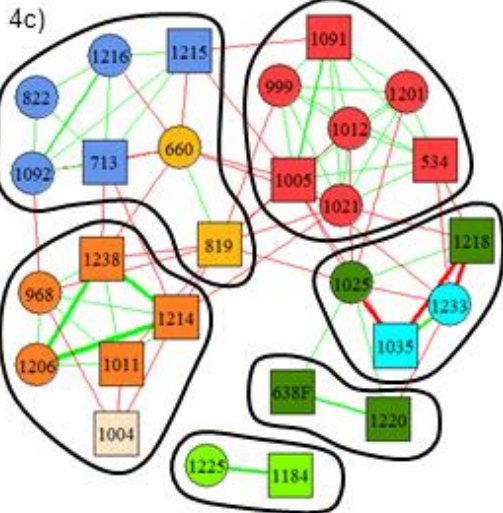
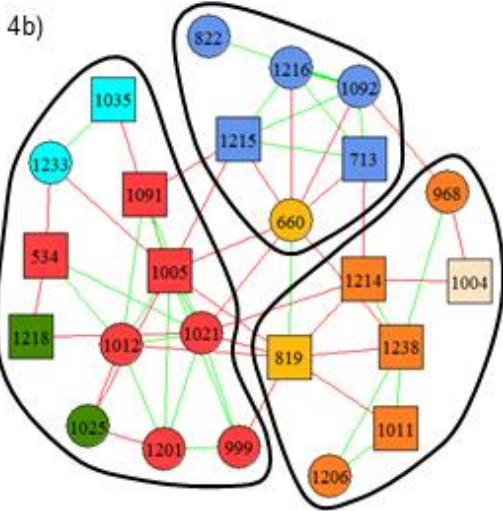
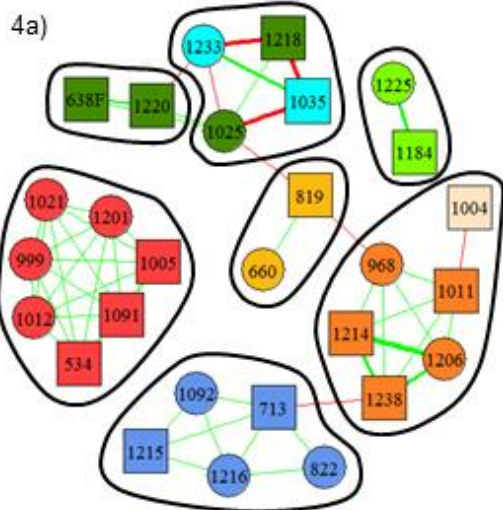


Figure 4. Network patterns from week two co-locations at: a) setts; b) latrines; c) setts and latrines combined ('All'). Node numbers, shapes and colours depict badger IDs, gender (square=female, circle=male), and social-group affiliation from trapping (light-blue=BP, dark-green=SH, light-green=BB, red=PO, gold=P, fawn=M2, orange=JH, dark-blue=W), respectively. Edge thickness is proportional to co-location duration. Edge colour indicates intra- (green) vs inter-social-group (red) co-locations. Black borders indicate network 'community' estimates (from Fast-Greedy algorithm).