

Article

Push and pull factors driving movement in a social mammal: context dependent behavioral plasticity at the landscape scale

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Abstract

Understanding how key parameters (e.g., density, range-size, and configuration) can affect animal movement remains a major goal of population ecology. This is particularly important for wildlife disease hosts, such as the European badger *Meles meles*, a reservoir of *Mycobacterium bovis*. Here we show how movements of 463 individuals among 223 inferred group territories across 755 km² in Ireland were affected by sex, age, past-movement history, group composition, and group size index from 2009 to 2012. Females exhibited a greater probability of moving into groups with a male-biased composition, but male movements into groups were not associated with group composition. Male badgers were, however, more likely to make visits into territories than females. Animals that had immigrated into a territory previously were more likely to emigrate in the future. Animals exhibiting such “itinerant” movement patterns were more likely to belong to younger age classes. Inter-territorial movement propensity was negatively associated with group size, indicating that larger groups were more stable and less attractive (or permeable) to immigrants. Across the landscape, there was substantial variation in inferred territory-size and movement dynamics, which was related to group size. This represents behavioral plasticity previously only reported at the scale of the species' biogeographical range. Our results highlight how a “one-size-fits-all” explanation of badger movement is likely to fail under varying ecological contexts and scales, with implications for bovine tuberculosis management.

Key words: dispersal, socio-biology, wildlife biology, wildlife disease, *Meles meles*, social groups, territoriality, perturbation, bTB

Quantifying animal movements and dispersal dynamics are integral to understanding individual fitness and survival. In addition, knowledge regarding animal movements can also provide important information for conservation, species management, and disease

control (Cullingham et al. 2008; Tucker et al. 2018). Despite the importance of understanding animal movement strategies, they can be particularly difficult to characterize due to their variable nature (Bowler and Benton 2005; Davidian et al. 2016; Tucker et al. 2018).

Movement strategies may be fixed and unconditional (i.e., without regard to environmental conditions). When individual movement strategies are conditionally dependent, however, they are generally more adaptive, intricate, and advantageous to fitness (Bowler and Benton 2005). The functional causes that promote conditional animal movement and dispersal can be proximate (i.e., population density; food availability; inter-specific interactions; relatedness: see Matthysen 2005; Bowler and Benton 2005; Morales et al. 2010; Davidian et al. 2016) or ultimate (i.e., inbreeding avoidance; kin interactions; habitat variability; intrinsic patch quality). For instance, in spatially structured populations, dispersal alleviates inbreeding depression (Greenwood 1980; Lambin et al. 2001). The drivers of animal movements may therefore be characterized as “push-pull” factors (Loe et al. 2009). Push-factors include the optimization of access to key resources (e.g., food and mates), whilst pull-factors may include the evasion of risk (e.g., predation, habitat change, and disturbance/perturbation). At the population level, this can lead to the emergence of source-sink dispersal dynamics (Diffendorfer 1998).

Recent investigations reveal that the criteria determining animal movement patterns are non-random, depending on both external information (condition dependence) and internal states (phenotypes or “personality” syndromes) (Bowler and Benton 2005; Cote et al. 2010; Wolf and Weissing 2012). This leads to qualitative differences between “disperser” animals, differentiated by their ability to colonize new areas. The result is the emergence of animal dispersal syndromes (Clobert et al. 2009). This is particularly apparent in spatially structured populations (Cote et al. 2010), where permeability to movement can vary locally (Hamilton’s “population viscosity”; 1964). Knowledge of the factors driving patterns of movement is therefore important for understanding the adaptive significance of processes underlying both reproductive behavior, and social dynamics (Bowler and Benton 2005; Nathan et al. 2008; Davidian et al. 2016).

Investigations into the variation in the movement dynamics of terrestrial mammals, especially small carnivores, at large landscape scales are challenging and rare (Bowler and Benton 2005). To address this, we utilize an extensive European badger *Meles meles* mark-recapture data set, collected more than a 4 year period across a 755 km² region of Ireland as part of a wildlife vaccination trial (see Aznar et al. 2011). Badgers have often been used as a model species for behavioral and ecological analysis (Stopka and Johnson, 2000; Macdonald et al. 2015). This is due to the variable extent to which populations can be group-living within discrete territories, with substantial flexibility in their social structure, as has been reported across their biogeographical range (facultative sociality; Johnson et al. 2002; Byrne et al. 2012a). For example, in lowland Britain, badgers can form large groups (e.g., >20 members) at high densities with well-defined territories (Johnson et al. 2002). Elsewhere, for example in Spain, territories can be large, loosely demarcated, and used by small social groups (e.g., 3 members). Indeed, a meta-analysis has found that badger movement propensity and distance was influenced by the overall population density (Byrne et al. 2014a), with “looser” territoriality described in lower density populations. Generally, groups form through natal-philopatry (i.e., offspring remaining in the territories they are born into; see Macdonald et al. 2008). Mark-recapture studies in high-density populations (Rogers et al. 1998; Macdonald et al. 2008) suggest permanent dispersal rates are relatively low (12–16%). Despite this, genetic pedigree studies demonstrate high levels of extra-group paternity (up to 50%; Dugdale et al. 2007).

Understanding badger movement is also important because the badger is a wildlife host of *Mycobacterium bovis*, the causative agent of bovine tuberculosis (bTB). Badgers have been implicated in the epidemiology of this zoonotic pathogen among cattle herds in Britain, Ireland, France, and Spain (Gortazar et al. 2012). Badger movements have been directly related to bTB risk in an undisturbed badger population (Rogers et al. 1998; Vicente et al. 2007), with a positive correlation between badger movement and the incidence of bTB at individual and social-group levels. Attempts to control the spread of bTB through badger culling have led to population density reduction, but also to the perturbation of social structure (O’Corry-Crowe et al. 1996; Tuytens et al. 2000). Where badgers survive culling operations, genetic studies suggest that their inter-territorial movements increase (Pope et al. 2007), which could potentially exacerbate the spread of bTB.

In this study, we aimed to test three main hypotheses. Firstly, that individuals may be more likely to move (immigrate) into relatively smaller (less competitive) groups, or groups exhibiting skewed sex ratios rather than those with balanced sex ratio composition. Thus, “pull factors” may attract one sex to groups with more of the other sex, to maximize opportunities for mating and increase potential reproductive output, that is, opportunity optimization. In contrast, competitive “push factors” may drive individuals to emigrate from their original groups, that is, competition driven emigration. For example, intense local resource competition (*sensu* Silk 1983) may arise among females for breeding resources when they predominate group composition sex ratios, whereas intense competition will arise among males for access to breeding females, when males predominate.

Secondly, we hypothesized that age and/or sex may influence inter-territorial movement probability, focusing on whether past movement history was a useful predictor of future movement. Evidence supporting this effect would suggest phenotypic dependent dispersal (Clobert et al. 2009). Finally, we hypothesized that some individuals might be frequent repeat movers (*itinerant* or “floaters” phenotypes; *sensu* Revilla and Palomares 2002), and that this propensity could be associated with reproductive tactics or group-specific characteristics. These animals may be important to identify as they may pose disproportion risk for disease spread.

Materials and Methods

Region and study population

This study was undertaken in County Kilkenny, in the south-east of the Republic of Ireland (around 52.6° N, 7.4° W; 2009–2012); utilizing data primarily intended to investigate the efficacy of a vaccine for bTB (see Aznar et al. 2018). The total study area was 755 km², making it the most geographically extensive mark-recapture project undertaken in badgers to-date. Approximately 75% of the study area was farmed (improved grasslands and tillage), interlaced with a network of hedgerows and small patches of woodland (ca. 10%), flanked to the east by the River Nore (Byrne et al. 2012b; 2014b) with a mean population density of 46 people km⁻². The vast majority of the site lay between 50 and 150 m above sea level (asl); previous research found badger occurrence was highest at elevations of 30–170 m asl (Byrne et al. 2014b). There were no mountains in the study area. One area (Slieveardagh), flanking the western border, had low hills reaching approximately 250 m asl at their peaks. The city of Kilkenny was not included as part of the study area. The average badger population density across the whole site was estimated at 0.8–1.1 km⁻² (Byrne et al. 2012b; L. Rosen, pers. comm.). This typifies low-medium badger density for pasture

dominated landscapes in Ireland (typically 1–3 badgers km⁻²; Sleeman et al. 2009; Byrne et al. 2012a, 2012b), but greater than typically reported in continental Europe (0.5–1 badgers km⁻²; Kowalczyk et al. 2000; Lara-Romero et al. 2012), and lower than in southern Britain (5–6 badgers km⁻²; Judge et al. 2017). However, there was variation in relative sett (burrow) density across the landscape (Byrne et al. 2014b, 2018; Supplementary Figure S1), partially attributable to variation in landscape suitability (Supplementary Figure S2), but potentially also due to former persecution and government-sanctioned culling operations occurring prior to the study (see Byrne et al. 2014a for details, and below). Our study area was not culled for 2 years prior to beginning this project (Aznar et al. 2011), with no culling being undertaken during the 4 years of study (Gormley et al. 2017). Furthermore, one third of the site was protected from culling during an adjacent large-scale intervention from 1997 to 2002 (Sleeman et al. 2009). Research from a culled badger population in Gloucestershire, UK (undisturbed density ca. 4.5 km⁻²) has shown that badger population density can recover from culling in less than 2 years (Tuytens et al. 2000). Other details about this region's resident badger population, associated with a vaccine trial, have been presented in Aznar et al. (2011, 2018), Byrne et al. (2012b, 2014a, 2018), Gormley et al. (2017), and Martin et al. (2017).

The site was surveyed for badger activity at setts and runs (frequently used badger paths), twice per annum between 2009 and 2012 ("capture sessions" see Byrne et al. 2012b; Martin et al. 2017 for more details). Setts were characterized as "main" or other. Main setts are large, complex structures, and there is typically only one per group territory (Byrne et al. 2012a). Badger captures were made primarily using wire stopped restraints (96%), supplemented by cage-trapping (4%), to enhance the capture of cubs (which can slip through restraints; Byrne et al. 2012b). Traps were deployed to maximize capture probability (Byrne et al. 2012b; Martin et al. 2017), by targeting sett locations and runs that exhibited evidence of badger presence, using a designed "activity score" based on indicators including number of active holes, spoil, fresh bedding, latrines presence, hairs, etc. (Martin et al. 2017). Byrne et al. (2013) showed that higher capture numbers were associated with several field signs (e.g., presence of rooting, latrines, and badger paths), and that the number of active sett openings was a predictor of badger counts. More traps were deployed than the anticipated number of resident badgers, resulting in 5–20 traps laid per sett per trapping session (e.g., during badger trapping operations in Ireland typically 10.6 [SD 6.5] traps are laid [Byrne et al. 2013]).

Once caught, badgers were anaesthetized, and examined to record sex and age class. Age class was based on tooth wear and coded as juvenile, adult, or old (Macdonald et al. 2009). Aging badgers in the field is challenging and somewhat uncertain; however, juveniles were inferred to be approximately <18 months, adults >18 months to <4 years, and "old" badgers >4 years old. At first capture, individuals were micro-chipped with radio-frequency identification (RFID) tags and tattooed for re-identification. Mortality events were also recorded, primarily caused by road traffic accidents (RTAs), and where badgers were marked, their RTA location records were recorded (Byrne et al. 2012b). Our dataset did not include full capture session data after the fifth capture session (in contrast with Gormley et al. 2017 that used a different subset of these data to look at oral vaccination strategy).

With regard to animal welfare, both trapping procedures present a low risk of injury (Byrne et al. 2015) and were approved under Irish legislation. The capture of badgers for this vaccine trial was

conducted under licenses (1876 Cruelty to Animals Act) issued by the relevant authorities (DHC, B100/3187; Department of Agriculture, DAFM, RL/08/06), and approved by the University College Dublin animal ethics committee (Animal Research Ethics Committee (AREC)-P-08-26).

Assigning site of residency, inferring group size indices and spatial structures

Badger movement was defined by individual capture histories (see Byrne et al. 2014a, 2018), consequently only badgers with >1 capture could contribute to movement metrics.

To depict the structure of the population, we inferred badger spatial group territories across the study population using Dirichlet tessellations (described in Byrne et al. 2018). Tessellations were constructed by drawing perpendicular straight lines at the half-way point between main setts and linking these points to form polygons (Hammond and McGrath 1998; Blackwell and Macdonald 2000; Delahay et al. 2000; Halls et al. 2001; Woodroffe et al. 2009; Roper 2010). The resulting polygons have been used to estimate the broad configuration and extent of badger territories (e.g., Hammond and McGrath 1998; Woodroffe et al. 2009), and this approach has proved reasonably congruent with empirical data (but see Delahay et al. 2000). Finally, we also implemented a constraint condition for low-density populations (following Halls et al. 2001), allowing a maximum distance from the main sett to the tessellation edge of 2 km (Byrne et al. 2018), and utilized additional badger sett location data outside of the study area to infer territory shape along the border of the study area (Byrne et al. 2014a).

Badgers were assigned to territories based on their capture locations (GPS acquired) across the landscape. If a badger was captured inside an inferred territory based on tessellations, then that badger was assigned to that territory for that capture record. Because 81% of badger recaptures were at main setts (638/792), their assignment to spatial groups was unambiguous in the majority of cases. Furthermore, as the nearest neighbor distance between main setts was ca. 800 m–1 km (Byrne et al. 2014a; McGrath G, personal communication), with the majority (73%; Byrne et al. 2014a, 2018) of recapture movements at shorter distances than this. Due to this, movements recorded during this study had a low risk of being categorized incorrectly as inter-territory.

We calculated a single index of group size over the full study period to facilitate our modeling approach, and thus avoid time-dependence. This index was based on the minimum number of unique animals alive (counts) that were captured over the study period within each inferred territory (Sleeman et al. 2009) – note, this also included animals that were only recorded once (as used elsewhere e.g., Van Apeldoorn et al. 2006). Previous work from this population found a significant positive correlation between point and aggregate total badger counts per territory ($P < 0.001$; Byrne et al. 2018). Singleton captures were retained, as these were a common capture history category across the whole study (56% of badgers across the 223 territories were captured once). Singletons were broadly distributed across group sizes (e.g., groups with ≤ 5 badgers = 63% singletons; >5 badgers 50% singletons), increasing sample size and statistical power. A previous analysis found that the cumulative effects of repeated trapping more than 4 years resulted in 79% of adult badgers in this study population being marked (Byrne et al. 2012b; note, in a high-density population there was a robust relationship between 3 years of capture data and long-term group size means; Noonan et al. 2015). Therefore, we aggregated across

capture sweeps to improve on the proportion of badgers trapped and marked (trappability). Nevertheless, cubs were under-represented in this dataset, due to slipping through wire stopped restraints (Byrne et al. 2012b), but were retained in the group statistics when captured. Of the badgers captured during the trial, 30% were first captured as juveniles (<18 months; Byrne et al. 2012b). The sex ratio composition of groups was based on unique badgers only (not including recaptures) and was calculated as the percentage of the group that was male (0% male to 100% male composition).

Effect of group composition on movement

To test the effect of group composition on push-pull factors, we built multivariable models controlling for significant confounding variables (e.g., time period between captures). The response variable was a binary outcome, representing whether an animal changed territory affiliation (therefore all animals with one or more captures were represented; dyads). Using a locally weighted scatterplot smoothing (LOWESS; polynomial regression), the functional relationship between the response variable and sex ratio, suggested the form was curvilinear, and best modeled as a quadratic term without the linear trend (note, additional linear models for each sex, respectively, were investigated and presented in [Supplementary Material S1](#)). Note: the LOWESS was only used to explore these data, not for inference. We also investigated the effects of age class, sex, and group size on push-pull factors. We controlled for the variation in the time period between captures by including inter-capture period as a linear nuisance variable across all models (Byrne et al. 2018). We removed recaptures occurring fewer than 4 days after initial capture, because badgers can behave atypically in the days immediately after capture and restraint (Schütz et al. 2006). We ran 2 suites of models including: 1) all data for groups; and 2) limiting only to groups with mixed sex composition. We ran the latter model to account for the problem that the probability of a female being recorded in all male groups would reach zero, and vice-versa; therefore, biases would be introduced in the parameter estimates in extreme group composition situations.

Animal movement history effects on future movement patterns

We built models where the future emigrant status of a badger was a binary outcome variable (1 = subsequently captured at a different territory to previous territory; 0 = subsequently captured at the same territory to previous territory). Consequently, only badgers with a minimum of 3 records (triplets) could contribute to this dataset (see also similar movement rules in [Macdonald et al. 2008](#)). Consequently, this dataset comprises badgers that had a previous record (at capture record-1; i.e., a binary immigration status of 1 if caught previously at a different group and 0 if caught at the same group as the current observation) and a future record (at capture record + 1; i.e., an emigration status). Predictor variables included immigration status (binary), age class (binary; young/adult vs. old), group size index, and sex.

The itinerant or “floater” phenotype

We categorized observations for individuals caught at least 3 times into 5 “itinerant classes”:

Class 1: “Residents”—individuals with a triplet record with 3 captures in the same territory (previous, current, and next capture sequence).

Classes 2–4: “temporary mover” triplets with trapping histories encompassing 2 territories, either of ABB, AAB, and ABA, respectively ([Supplementary Figure S3](#)).

Class 5: “floaters/itinerant”—individual triplets with a different fidelity on each recapture (ABC).

We modeled the probability of recording a residency pattern (AAA) relative to a floating pattern (ABC) using random-effects logit mixed model—where random effects applies to the animal, as each animal can have more than one “triplet” of observations, and the social-group/territory during the present capture (i.e., not the territory immigrated from, nor the territory emigrated to). Again, we modeled independent variables as fixed effects, including sex, age class, group size, and time difference (time since last capture).

Overall modeling approach

All investigations used generalized linear mixed models (GLMM). Response variables were binary outcomes and were modeled using a logit link function ([Hosmer et al. 2013](#)). These were modeled at the individual-movement level, with repeated movements by the same individual, and with individuals potentially being recorded within differing social group territories across capture events. We therefore fitted a cross-classified random effect (animal-id and territory-id random-effect interaction term), due to the non-nested nature of these records [i.e., this was not a simple hierarchical multi-level model ([Rabe-Hesketh and Skrondal 2008](#))]. To test whether these random effects were significant, we used a likelihood ratio test to assess if the variation in the intra-class correlation (ρ) among groupings was zero ([Gutierrez et al. 2001](#)). Each of our hypotheses was investigated by fitting both univariable and multivariable models. Competing models were evaluated using Information Criteria. Information criteria generally take the form of:

$$IC = -2\ln(L) + a * s$$

where a is a penalty term and s is the number of parameters to be estimated. L is the likelihood estimation of the model. Two ICs were used in the study, Akaike’s information criterion (AIC) and Bayesian information criterion (BIC; also known as Schwarz Information Criterion). The main difference between the BIC and AIC pertains to the penalty parameter, which is generally set to 2 for AIC and $\log(N)$ for BIC. When comparing candidate models, the most supported models had the lowest IC values ([Burnham and Anderson 2003](#)). Where outcomes conflicted between AIC and BIC model ranking, we conservatively chose the most parsimonious model ([Dohoo et al. 2009](#); please note additional competing models within the [Supplementary Material](#)). First order interaction terms between independent variables were assessed where biologically plausible, and retained if they improved the model, and if the odds ratio for the interaction term (i.e., the exponentiated estimated β) in the model had a 95% CI that did not straddle 1 ($P < 0.05$). All models were fitted in Stata SE version 14 (Statacorp 2015, USA).

Results

The mean ($\pm$ SD) number of unique animals captured per territory was 5.06 ± 2.43 (IQR: 4–6; Max: 15) badgers per inferred territory ($N = 223$). The mean inferred territory area within the core was $2.74 \pm 1.40 \text{ km}^2$ (range: 0.4–8.3 km^2 ; non-overlapping with study boundary). This led to significant variation in the density of total captures across the core study area from 0.14 badgers km^{-2} to 11.61 badgers km^{-2} (see [Byrne et al. 2018](#)). Overall, we recorded

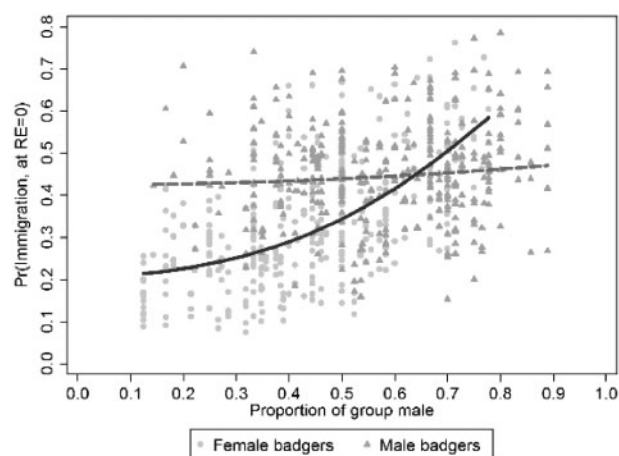


Figure 1. The predicted relationship between the probability of a badger immigrating into a badger group and the sex ratio within the recipient group, as measured by the proportion of the group that is male. The mean predicted probability of being an immigrant is represented by a black line for female badgers and grey dashed line for males. These predictions are from a random-effect (RE) logit model.

827 badger repeat captures (i.e., 2 record dyads) for 463 individual badgers. Univariable associations are presented in [Supplementary Material \(S3\)](#).

The effects of group composition, group size, and sex on immigration

The probability of an individual immigrating into a group was significantly greater for male relative to female badgers ([Table 1](#); adjusted odds ratio [OR]: 2.30; $P = 0.02$); the majority of immigrant badgers were male (59.5%), whereas the majority of individuals fidelitous to their original group territory were female (67.3%). There was a significant negative association between being a recent immigrant and increasing recipient group size, with the odds of a badger being an immigrant decreasing by 10% with each additional recipient group member recorded (adjusted OR: 0.90; $P < 0.01$). This indicates that larger groups tended to have less inward migration: 47.6% of immigration movements were into social groups with < 5 members (obs. $N = 109$), whereas 24.7% were into large groups of ≥ 10 members (obs. $N = 21$). “Old” badgers (inferred to be approximately > 4 years) were significantly less likely to change group affiliation than younger age classes (grouping of juvenile and adult categories; adjusted OR: 0.49; $P < 0.01$); 24.4% of badger records for “young” animals (< 4 years old) showed a territory affiliation change, whereas only 15.3% of old badgers recorded movements. Group composition had, overall, a significant non-linear impact on the probability of changing group territory affiliation (proportion male within the group; $P < 0.01$), however the most supported model suggested that this effect depended on the sex of the immigrant. The probability of a female badger being an immigrant to a group was significantly greater with increasing male sex ratio bias within the recipient group (proportion male, modeled as a quadratic term; OR: 14.88; $P < 0.01$; [Figure 1](#)). Group sex ratio did not have a significant effect on immigration probability for male badgers (OR: 2.38; $P = 0.16$; [Figure 1](#)). Qualitatively similar results were found when separate models were fitted for each sex, and when modeling sex ratio as a linear predictor (see [Supplementary Material S1](#); however, a separate model for male emigration suggested males had a higher probability of moving

Table 1. Multivariable random-effects (RE) logit mixed model explaining variation in the probability of badgers immigrating into all social groups (obs. $N = 827$)

Immigration	OR	95% CI	P
Sex.female	Ref.		
Sex.male	2.30	1.12–4.75	*
(Proportion of group male) ²	14.88	2.24–98.66	**
Sex*(Proportion of group male) ²	0.16	0.02–1.48	^
Group size	0.88	0.82–0.95	***
Time between captures (per 10 days)	1.02	1.02–1.03	***
Age class.young	Ref.		
Age class.old	0.47	0.28–0.79	**

The proportion of group that was male was modeled as a quadratic term., $P = 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Conservative likelihood-ratio test of RE: χ^2 (DF: 1) = 9.59; $P = 0.001$.

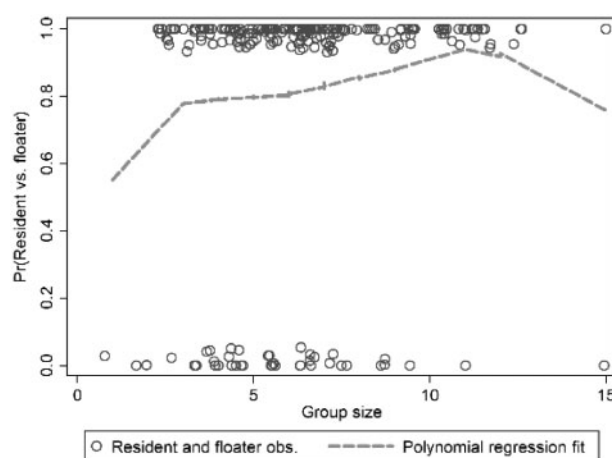


Figure 2. The relationship between badger group size and the associated probability of resident (AAA) or floater (ABC) movement triplet patterns. The probability of a resident pattern (coded 1) increases in groups with larger group membership; reciprocally, floater patterns (coded 0) are more likely in smaller groups. Trend demonstrated by dashed line using a LOWESS polynomial regression line.

away from groups with a higher male sex ratio). Restricting the dataset to only mixed-sex groups (i.e., sex ratio was neither 0% nor 100% male), also gave similar results (see [Supplementary Material S2](#), and [Supplementary Table S1](#)).

Triplets—the itinerant phenotype

Overall, 405 observations had both preceding and subsequent (triplet/triad) capture histories, made by 231 badgers across 160 groups. The most common (re-)location typology was a pattern of consistent group territory residency (AAA), as seen in 181 observations (181/405; 44.7%) involving 119 badgers (119/231; 51.5%). Temporary mover typologies varied by pattern involved (10.62%–18.3%), but overall accounted for 183 observations (183/405; 45.19%), involving 172 individuals (172/231; 74.5%). The floater/itinerant movement typology was least common, involving only 10.6% (43/405) of observations by 37 badgers (37/231; 16.0%).

The most supported random-effect multivariable model included sex ($P < 0.01$), group size ($P = 0.04$), and contained the nuisance variable for time difference between captures ($P = 0.02$). Females were significantly more likely to display longer-term group fidelity (90.9%)

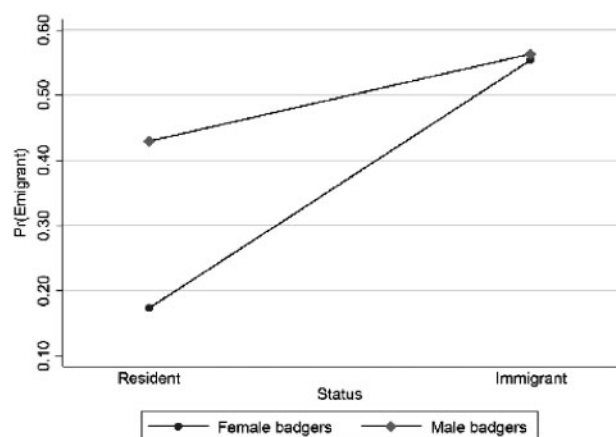


Figure 3. The marginal predicted probability of a badger being an emigrant (outward movement from territory) relative to its sex and previous immigrant status ("status"), from a random-effects logit model.

relative to males (67.8%). The modeled probability of a residency pattern was greater with larger group size (adjusted OR: 1.60; Figure 2); and thus floaters/itinerants were more likely associated smaller group sizes. For groups with >10 members recorded, 7.4% of observations involved floaters and 92.6% "residents." In contrast, groups with <5 members recorded, 23.6% were floaters and 76.4% were residents.

Effect of previous movement history on emigration status

The most supported multivariable model indicated that subsequent movement probability was most significantly affected by recent immigration status, sex and an interaction of these factors (obs. 405; $P < 0.001$). Overall, males were on-average significantly more likely to emigrate (adjusted OR: 5.245; $P < 0.001$) than females. Moreover, individuals that were immigrants into a group were significantly more likely to subsequently emigrate from that group ($P < 0.001$); although, this effect was mainly driven by female badgers (immigrant*sex; $P < 0.001$). Overall, 53.2% of previous immigrants subsequently became emigrants, whereas 26.7% of non-immigrant badgers proceeded to emigrate. This difference was significantly greater for females than males (Figure 3); the odds ratio (OR) for female immigrants to be a subsequent emigrant was 7.90 ($P < 0.001$), whereas for male immigrants the OR was 1.41 ($P = 0.222$, i.e., being a previous immigrant did not have a significant impact on male badgers likelihood of moving again). Females with a history of previous immigration into new groups during the study period were substantially more likely to emigrate later during the study than were resident females. 54.2% of immigrant females moved on their next recorded movement; whereas only 13.0% of "resident" females did. For males, 52.5% of former immigrants later emigrated, whereas 44.0% of initial group residents did, although this difference between males was non-significant ($P > 0.2$).

Discussion

We found support for all 3 of our hypotheses, where badger movement dynamics were influenced by: 1) the size and composition of the group individuals move into; 2) the characteristics of the animals (sex, age) moving; and 3) individual movement histories (i.e.,

previous movement behavior), such that different behavioral typologies could emerge.

We also demonstrated for the first time that large variation in the socio-spatial dynamics (movement in terms of group size) across one large contiguous agri-dominated landscape can occur for this species.

Specifically, we found that the probability of an animal moving into a territory decreased significantly with an increase in the index of group size (hypothesis 1). Overall, our study area was almost fully saturated with badger territories (see [Supplementary Material](#)), varying only in local density (clines) of territory occupancy. Badgers, however, exhibited a lower propensity to move between setts in higher density parts of the study area (where group sizes were also larger). When movements were recorded in these higher density areas, they tended to be of shorter distance ([Byrne et al. 2018](#)). As predicted by Hestbeck's social fence hypothesis ([Hestbeck 1982](#)), we observed that higher immigration rates were recorded into smaller groups (47% in groups of <5 individuals) relative to larger groups (25% in groups of ≥ 10 individuals). This indicates that larger groups may be more inherently stable than smaller groups, which appear more fluid (but see limitations below). Research from high-density populations report a similar relationship, with more inward badger movements being associated with smaller groups ([Rogers et al. 1998](#); [Macdonald et al. 2008](#)).

A second important factor determining inter-group movement patterns was relative sex ratio. When females moved they were more likely to move into recipient groups, biased towards males. In contrast, male immigration probability was not associated with recipient group sex ratio. A separate model of male emigration did, however, reveal that males exhibited greater probabilities of moving away from their original groups, when residing in male dominated groups ([Supplementary Material S1](#)). In high-density populations, males are typically more affected by the sex ratio, where they tend to be attracted to groups with a higher female sex ratio (although the trend in the Wytham population was $P = 0.055$; [Macdonald et al. 2008](#); [Rogers et al. 1998](#)). An earlier study in Wytham Wood ([da Silva et al. 1994](#)) found no relationship between dispersal and the numbers of males or females within groups. This suggests that push/pull patterns vary temporally.

Our results suggest that sex might influence future movement propensity (hypothesis 2), and that male badgers moved more often than females (60% males exhibited some movement vs. just 33% of females). Male badgers also exhibited less group fidelity per individual (males 68%; females 91%). This supports previous work by [Rogers et al. \(1998\)](#) who found that males were less likely to be "non-movers" than female badgers (37% male non-movers, 70% female non-movers) in the Woodchester Park badger population. In Wytham Woods, a male bias in badger movement has been recorded, although not a bias in permanent dispersal probability ([Macdonald et al. 2008](#)). Indeed, studies by [Cheeseman et al. \(1988\)](#), [Kruuk and Parish \(1987\)](#), and [Harris and Cresswell \(1987\)](#) in Britain all showed that dispersal rates for males exceeded those for females. In terms of dispersal movements (defined heuristically as movements >1 km) from the Kilkenny population, [Byrne et al. \(2014a\)](#) have reported previously that there was a significant difference in the dispersal kernels between male and female badgers. Here males undertook such movements more frequently, but females tended make proportionally greater long-distance dispersal attempts.

In terms of previous movement history (hypothesis 3), we found that badgers that had moved previously were significantly more

likely to move again; although we cannot discount the fact that a proportion of such triplet movements included animals that returned to their original territory (18.3%; ABA typologies). Rogers et al. (1998) also reported a similar finding in Woodchester Park.

We observed movement typologies ranging from “non-movers”, to occasional movers, to “itinerant” badgers, but again, these patterns were linked strongly to group size. Younger individuals, that potentially had not yet established permanent group residency, were more likely to be itinerant. Elsewhere, urban badger populations have been reported to appear fluid in terms of inter-group movements, with 28–30% of adult badgers undertaking temporary visits to non-group setts (Huck et al. 2008). This has led to the concept of urban “super-groups” with overlapping group ranges, and a bias toward “floater” type phenotypes (Huck et al. 2008). Outside of Britain, a low-density badger population in Doñana, Spain, was reported to have a flexible social system, with male badgers making more frequent movements than females, but also that males tended to expand their territories given the opportunity to maximize the potential for mating (Revilla and Palomares 2002). Indeed, the authors of that study also describe a “floater” type female phenotype within their population.

The selection hypothesis (Hamilton 1964) is relevant in this context, where, if floating or itinerancy brings greater exposure to risk (intra-specific competition/fighting; failure to find resources in unfamiliar habitat, RTA risk, etc.), then badgers establishing permanent residency will ultimately come to predominate older age classes. Certainly, older individuals moved less often than younger individuals in our dataset (24% of adult movements involved a group territory change, whereas only 15% of older badgers undertook such movements). This contrasts with Rogers et al. (1998) who found that movements were more frequently associated with “older and heavier” badgers in Woodchester Park. In Wytham, no significant difference in age class and dispersal probability was apparent (Macdonald et al. 2008), although the highest probability of dispersal was recorded during the first year of life. Older, more settled animals could represent more dominant, or established individuals, as suggested for lower density populations in Spain (Revilla and Palomares 2002), nominally with descendants in their established group. Alternatively, they could be frailer individuals that would fail to challenge residents in other groups, and thus remain *in situ* to minimize potential conflict.

A key finding from this study was the substantial variation in important population parameters within one large contiguous landscape. As well as significant variation in local density (Supplementary Figure S2; Byrne et al. 2018) and group sizes across this study population, we also observed large variation in inferred territory size (range: 0.44–8.25 km²), suggesting that this population included all the full range of territory sizes reported for badgers across their European range (Kauhala and Holmala 2011). Our results demonstrate, for the first time, that a single landscape can support a very heterogeneous badger population, displaying significant variation in behaviors, and life-history tactics. Such variation has an impact on badger socio-biology and movement dynamics (Byrne et al. 2014a; present study), and can ultimately affect pathogen transmission.

Limitations

A caveat to this work is that the frequency of trapping used here is only able to detect minimal movement rates. Detecting more frequent movement “forays” would require more intense trapping, or active tracking. It is therefore possible we underestimated the true

number of “floater” movement patterns within our population. In contrast, because setts were dispersed and main setts were centrally located within territories in our study area, the likelihood of assigning captured animals to territories incorrectly was lower than in higher density populations where territories are tightly packed at smaller spatial scales.

Estimating group size with precision is very challenging, especially at the scale undertaken by this study. We enumerated unique animals captured per territory to derive an index of group size over the study period. Nevertheless, we acknowledge that this index is likely positively biased relative to the true (but unknown) mean group size, and that this could mask the stability of group size over time. Other studies have also used this enumeration approach with badger groups (e.g., Van Apeldoorn et al. 2006; Sleeman et al. 2009), whereas others have used the Minimum Number Known Alive (MNA) index to estimate group size (e.g., Macdonald et al. 2009; Rogers et al. 1998). Despite this, MNA is also known to be a negatively biased estimator (Byrne et al. 2012b). Although we found that larger groups had a lower probability of inward migration, under different circumstances both large and small groups could be stable or unstable with high turnover, which would not be depicted directly by our index. Previous work from this same population found a significant correlation ($P < 0.001$) between annual indices of group size and aggregated (multi-annual) metrics, with little impact on the parameter estimates in the impact of density on movement metrics when tested (Byrne et al. 2018). Nevertheless, these annual indices are known to be negatively biased indicators of group size. Ultimately, we advocate that future studies employ additional independent means to enumerate group sizes where logistically feasible, which is often not the case at very large spatial scales.

Context and implications for bTB

In conclusion, we found support of group size-, sex-, and age-specific push and pull factors impacting on badger movements, which occurred with relatively high frequency across a heterogeneous population. Moreover, we discovered that these movement traits varied enormously within this landscape, ranging in character from patterns seen in high-density southern British badger populations, through to patterns typifying low-density badger populations in Spain.

These findings challenge the traditional view depicting more stringent territoriality for badgers (e.g., Kruuk 1978; Woodroffe et al. 2006) and fills an important knowledge gap about the cline in badgers movement dynamics inferred from fluid low-density socio-spatial arrangements (e.g., Revilla and Palomares 2002) through to high-density populations (e.g., Rogers et al. 1998; Macdonald et al. 2008).

Crucially, group inter-connectivity is relevant to badger management (culling) in response to bTB herd breakdowns in sympatric cattle populations. For instance, perturbing the badgers’ socio-spatial system can result in enhanced rates of inter-group interactions, potentially leading to increased disease spread (Macdonald et al. 2015). Our results show that badgers, in the absence of active culling, can exhibit highly variable flexible social structures across agri-dominated landscapes. Such fluidity may in fact dampen the effect size of culling induced perturbation, with bTB being less constrained by group territoriality (Olea-Popelka et al. 2005). Therefore, perturbation may be additive to an already dynamically interactive population. Indeed, while social perturbation (measured as an increase in movement patterns) following culling operations has also been evident in Ireland (O’Corry-Crowe et al. 1996), no evidence for any increase in badger or cattle bTB prevalence according with

the perturbation hypothesis has been recorded to date (More and Good 2015). Irrespective of the underlying dynamics, fluidity in population social structuring, linked to increased movement, could facilitate pathogen dispersal. Therefore, effective interventions that do not disturb social structure (e.g., vaccination) may be prudent longer-term solutions (Aznar et al. 2018). Future research should include modeling how these fundamental parameters impact patterns of infection (bTB) within this badger population and compare these findings with other contemporary landscape scale studies across a variety of ecological and disease contexts (i.e., differing densities and infection pressure).

Ultimately our detailed examination of badger movements on a broad landscape scale, exemplifies the complexities of mammalian dispersal syndromes generally. Importantly, although outcomes can appear similar, factors influencing male versus female strategies may be different (Pusey 1987), evoking recognition that “one size fits all” explanations of animal movement are likely faulty and incongruent with the drivers underlying patterns (Cote et al. 2010).

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Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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