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1 **Large-scale movements in European badgers: has the tail of**
2 **the movement kernel been underestimated?**

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21 **Summary**

- 22 1. Characterising patterns of animal movement is a major aim in population
23 ecology, and yet doing so at an appropriate spatial-scale remains a major
24 challenge. Estimating the frequency and distances of movements are of particular
25 importance when species are implicated in the transmission of zoonotic diseases.
- 26 2. European badgers (*Meles meles*) are classically viewed as exhibiting limited
27 dispersal, and yet their movements bring them into conflict with farmers due to
28 their potential to spread bovine tuberculosis in parts of their range. Considerable
29 uncertainty surrounds the movement potential of badgers, and this may be related
30 to the spatial-scale of previous empirical studies. We conducted a large-scale
31 mark-recapture study (755km²; 2008-2012; 1,935 capture-events; 963 badgers) to
32 investigate movement patterns in badgers, and undertook a comparative meta-
33 analysis using published data from 15 European populations.
- 34 3. The dispersal movement (>1km) kernel followed an inverse power-law function,
35 with a substantial 'tail' indicating the occurrence of rare long-distance dispersal
36 attempts during the study period. The mean recorded distance from this
37 distribution was 2.6km., the upper 95%ile was 7.3km and the longest recorded
38 was 22.1km. Dispersal frequency distributions were significantly different
39 between genders; males dispersed more frequently than females but females
40 made proportionally more long-distance dispersal attempts than males.
- 41 4. We used a subsampling approach to demonstrate that the appropriate minimum
42 spatial-scale to characterise badger movements in our study population was
43 80km², substantially larger than many previous badger studies. Furthermore, the

44 meta-analysis indicated a significant association between maximum movement
45 distance and study area size, while controlling for population density. Maximum
46 long-distance movements were often only recorded by chance beyond the
47 boundaries of study areas.

48 5. These findings suggest that the tail of the badger movement distribution is
49 currently underestimated. The implications of this for understanding the spatial-
50 ecology of badger populations and for the design of disease intervention
51 strategies are potentially significant.

52 **Key-words** *Meles meles*, dispersal kernel, mark-recapture, sex-biased dispersal,
53 landscape scale, bTB, culling, bTB vaccination, wildlife management

54

55 **Introduction**

56 Animal movement is one of the most important phenomena in nature (Nathan et al.
57 2008; Holyoak et al. 2008). Knowledge of animal movement affects our
58 understanding of fundamental ecological processes – for example genetic diversity,
59 population viability and range expansion – and has a major impact on how many
60 wildlife management and conservation issues are addressed (for example, attempts to
61 control wildlife disease or landscape management for migrating species; Cullingham
62 et al. 2008; Clobert et al. 2012). In general, ecological investigations tend to
63 concentrate on common population-level events, while rarer events within populations
64 are often ignored or assumed to be unimportant (Trakhtenbrot et al. 2005; Holyoak et
65 al. 2008). Long-distance dispersal attempts (LDDs) are, by their nature, infrequent but
66 can be extremely influential (Trakhtenbrot et al. 2005). For example, LDDs determine
67 the velocity of species spread across a landscape (Trakhtenbrot et al. 2005), which
68 have implications for the ability of species to track their climatic tolerance under a
69 rapidly changing climate (Schloss et al. 2009). Despite substantial advances in our
70 theoretical understanding of dispersal (Clobert et al. 2012), and decades of empirical
71 studies across a broad range of taxa, estimating long-distance movements generally
72 and LDDs in particular remains a major challenge.

73 In general, LDDs are important because they can connect disparate populations,
74 allowing for genetic connectivity, the colonization of vacant habitat across changing
75 landscapes and maintain global persistence in the face of local extinctions (Baguette
76 2003; Trakhtenbrot et al. 2005; Ronce 2007; Schloss et al. 2012). Over longer
77 temporal scales, LDDs can also be a major driver of evolutionary speciation (Ronce
78 2007 and references therein).

79 The occurrence of LDDs in animal or plant populations that harbor infectious disease
80 may also result in the rapid spread of disease (Cullingham et al. 2008; Mundt et al.
81 2009). While lasting effects of dispersal on genetic diversity requires successful
82 reproduction (Trakhtenbrot et al. 2005), there is no such absolute requirement for the
83 spread of disease providing there is a susceptible population and the possibility of a
84 transmission event occurring. Zoonotic disease transmission to domestic animals and
85 humans is currently a major issue in many parts of the world (Pech et al. 2010). In
86 disease control programs and field trials, the movement of infectious animals into an
87 area under disease control is often minimised through the use of barriers (*cordon*
88 *sanitaire*; Sleeman et al. 2009; Pech et al. 2010). These barriers can be physical, such
89 as rivers (e.g. Sleeman et al. 2009) or biological, such as buffer zones where the host
90 species is vaccinated (e.g. Pech et al. 2010). When designing biological barriers to
91 immigrating disease hosts, an understanding of the movement ability of the host,
92 including the ability of the host to pass through neighbouring territories, is required.
93 Often, the species dispersal kernel may inform an appropriate width for such a buffer
94 (Pech et al. 2010).

95 Badger (*Meles meles* Linnaeus) movements are of intense interest from pure and
96 applied disease ecology perspectives. Despite of their importance, there is little
97 known about the frequency of LDDs made by badgers, or whether they differ amongst
98 groups within populations (e.g. sex biases). Like other philopatric mammals,
99 dispersal in the badger may be important in avoiding inbreeding depression and may
100 be modulated by competition or facilitation amongst conspecifics (Greenwood 1980;
101 Macdonald et al. 2008). The frequency and length of dispersal movements may be
102 effected by density dependence (DD; Matthysen 2005), which can be a positive or
103 negative process. A positive DD relates to the movement of animals from high

104 densities to lower densities, with the consequence of reduced competition, increased
105 chance of survival and reproductive output. Negative DD suggests that high densities
106 result in lower dispersal propensity, due to the groups being socially constrained
107 (packed) by aggressive neighbours or where there are benefits to individuals to
108 aggregate at higher densities (Matthysen 2005 and see Le Galliard et al. 2005). The
109 length of dispersals will also be affected by the socio-spatial distribution of territories
110 and the distribution of resources (mates and feeding patches), which may affect
111 groups (e.g. genders, age-classes) within populations differentially (Rouce 2007).

112 Badgers are an important wildlife reservoir of *Mycobacterium bovis*, the causative
113 agent of bovine tuberculosis (bTB) in cattle, in Britain and Ireland (Griffin et al. 2005;
114 Bourne et al. 2007) and a bTB spill-over species in other countries (Spain and France;
115 Gortazar et al. 2012). Badger movements and dispersal attempts may facilitate the
116 spread and maintenance of bTB within badger populations (Rogers et al. 1998;
117 Vicente et al. 2007; Riordan et al. 2011) and also the transmission to, and from, cattle
118 (Donnelly et al. 2006). Population reduction through culling has been studied in both
119 Britain and Ireland as a means to reduce intraspecific and interspecific transmission of
120 bTB amongst badger and cattle populations (Griffin et al. 2005; Bourne et al. 2007).
121 Research has found that culling can disrupt the territorial behaviour of badgers
122 (increasing movement) that evade capture and neighbouring non-culled populations
123 (Tuytens et al. 2000a). It has been hypothesized that this perturbation of badger
124 populations can increase the risk of disease spread from badgers to cattle herds
125 (Donnelly et al. 2006; Carter et al. 2007). In high-density badger populations, there is
126 evidence of increased bTB risk to cattle herds up to 2km from a core badger removal
127 area, for up to two years post-cull (Donnelly et al. 2006; Jenkins et al. 2010). Due to
128 these findings, some proposed strategies to tackle bTB in badgers and cattle include

129 badger culling in core areas and vaccinating badgers in a ring of 2km in width around
130 the culled area (Smith et al. 2012). Other studies have used culling buffers of 3km or
131 more to reduce inward badger migration (Griffin et al. 2005; Sleeman et al. 2009).
132 Currently, there are no estimates of the proportion of badgers that could move
133 distances greater than 2 or 3km as an empirically derived dispersal kernel has yet to
134 be described. While the efficacy of such buffer zones will depend on many factors
135 (such as culling efficacy, starting density, natural barriers to movement etc.), the
136 dispersal kernel would allow one to estimate an appropriate minimum distance
137 required to ensure site independence to a defined acceptable threshold (Pech et al.
138 2010).

139 Here we use the largest spatial-scale mark-recapture study of European badgers
140 hitherto undertaken to investigate movement patterns in a medium-density population.
141 We used a repeat subsampling technique to estimate an appropriate minimum spatial-
142 scale for badger movement studies in medium-density populations. We fitted two
143 dispersal kernels to estimate the movement probabilities at various distances.
144 Comparisons between dispersal kernels were used to test: 1) if badger dispersal is
145 better characterized by a fat-tailed distribution over an exponentially bounded
146 distribution; and 2) if there was a gender difference between dispersal distributions.
147 We hypothesised that there would be a relationship between study area size and
148 maximum distance moved by badgers reported in the literature, and that this
149 relationship may be confounded by estimated local density. Thus, we reviewed and
150 modelled published data from studied badger populations across Europe to assess
151 whether there is a relationship between study area size and LDDs, while controlling
152 for density. We discuss the implications of the findings for our understanding of

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- 153 badger ecology and programs aimed at controlling the spread and maintenance of bTB
154 within badger populations.

155 **Materials and methods**

156 The study area was located in north-western Co. Kilkenny, Republic of Ireland
157 (52°40'N; 7°24'W), and extended over 755km². The eastern boundary of the study
158 area was delineated by the River Nore; a large river (~30m width at Kilkenny City;
159 Mean Annual Flow: 27.1 m³/s) that may represent an impediment (but not a barrier)
160 to badger movement, with the exception of bridging points (Sleeman et al. 2009).
161 Other boundaries were made up of smaller rivers or roads (non-badger impediments).
162 The land is low-lying at 60-180m ASL and soils are predominantly rich and well
163 drained. Approximately 75% of Co. Kilkenny is farmed (improved grasslands and
164 tillage), and divided by an extensive hedgerow network, while 9.8% of land cover is
165 forested. The mean population density is 46 persons.km⁻².

166 **Badger population**

167 Estimated mean badger density during the study period (based on mark-recapture
168 models) was approximately 1 badger km⁻² (true population densities may be slightly
169 higher if “untrappable” badgers are present; Byrne et al., 2012). Currently part of the
170 badger population outside of the study area in the Republic of Ireland is culled (see
171 Byrne et al. 2013a; Byrne et al. 2013b), though no culling has taken place in the area
172 for two years prior to the start of this study (Byrne et al. 2012). Approximately one-
173 third of this area (253km²) was part of a reference area in the Four Area Project (a
174 large-scale TB-related experimental project), where culling in response to herd
175 breakdowns was limited during the years 1997–2002 (0.06 km⁻² year⁻¹; Griffin et al.
176 2005). Badger populations can be disrupted for a period of time after culling, for
177 example, three years for a population of 4-8 badger km⁻² in Britain (Tuytens et al.

178 2000b). Given the lower densities in Ireland, we expected that a two-year no-cull
179 period would allow the population to recover to approximately pre-removal densities.
180 However, it is possible that the population structure was still recovering during the
181 initial period of the study.

182 Mark-release-recapture

183 An extensive mark-release-recapture (MRR) program was undertaken at the study site
184 between September 2009 and June 2012. All badger setts (complex subterranean
185 burrow systems) known from surveys were visited during six separate ‘sessions’, each
186 taking 20-24 weeks to complete, where an assessment was made of sett activity. Setts
187 were considered ‘active’ using combinations of multiple cues (presence of fresh spoil,
188 bedding, etc. and the absence of vegetation growth within the sett entrance (Byrne et
189 al. 2012; Byrne et al. 2013a)). Each active sett was trapped for 8 nights of capture
190 effort (Monday night–Thursday night over two sequential weeks) using a combination
191 of stopped body restraints (minimum closure: 28cm) and steel wire mesh cage-traps
192 (see Byrne et al. 2012). Traps were checked daily as early as possible and always
193 before 12pm to limit stress for any captured animals. The capture histories of badgers
194 marked and released during an additional training period between June 2008 – August
195 2009 were also included in the analysis (n=122 marked badgers during this period;
196 further details in Byrne et al. 2012).

197 Captured badgers were anaesthetised with ketamine hydrochloride (0.1 ml kg⁻¹) and
198 medetomidine (Domitor[®]; 0.1 ml kg⁻¹) administered by intramuscular injection by an
199 onsite veterinarian (Murphy et al. 2010). When first captured, each badger was
200 implanted with an identifying passive transponder and tattooed with a unique number
201 in the inguinal region. Badgers were placed in a wooden box with a ‘flap’ doorway

202 beside the sett of capture during recovery from the anaesthetic. This box was dark and
203 provided protection for the animal during the recovery phase. Marked dead badgers
204 (recoveries; e.g. due to road traffic accidents (RTAs)) inside or outside the study area
205 were recorded.

206 Movements were measured as the Euclidean distance (D) between recaptures (or
207 encounter points when using recoveries). True movement distances are likely to be
208 substantially greater as badgers typically move in tortuous routes (e.g. Loueiro et al.
209 2007). Also, there is a low temporal resolution within this dataset and therefore the
210 methodology is insensitive to detect temporary/transient movements. The data
211 collection has increased extent, and sample size, to the detriment of temporal
212 resolution. However, this does not invalidate our inferences as *i.* the underlying
213 process of badger dispersal may take long periods of time (Roper et al. 2003) *ii.* we
214 make inferences at the population scale (the scale at which the data was collected)
215 (Cushman 2010) *iii.* one of the movement models (Inverse Power Function) is robust
216 against marking frequency and effort, and can be used to make reliable proportional
217 dispersal estimates (Fric and Konvicka 2007). There is the potential for badgers to
218 make frequent short-term forays, and this could affect disease spread and other
219 ecological attributes at smaller temporal and spatial-scales (Macdonald et al. 2008).
220 The movements recorded therefore represent minimum distance travelled.

221 Ethics Statement

222 Work on badgers (trapping, marking and vaccinating) was approved by the University
223 College Dublin (UCD) Animal Research Ethics Committee (AREC) and met
224 appropriate guidelines for animal field studies (Sikes et al. 2011). The capture of
225 badgers was conducted under licenses (1876 Cruelty to Animals Act) issued by the

226 Irish Department of Health & Children. The capturing methods conformed to national
227 legislation for the humane trapping of wildlife (Wildlife Act, 1976, Regulations 2003
228 (S.I. 620 of 2003), Republic of Ireland). Capture via stopped body restraints or cages
229 result in very low rates of injury to badgers (Woodroffe et al. 2005a; Murphy et al.
230 2009). Throughout the study, on-site veterinarians monitored the health of captured
231 animals. Standard capturing protocol was employed during this study, where traps
232 were laid by experienced field staff in a manner that would maximise the probability
233 of badger capture (e.g. at active sett openings).

234 Effect of study-scale on movement metrics

235 We used a subsampling technique with a circle-sampling frame to investigate the
236 effect of study-scale on metrics of badger movements (Franzen and Nilsson 2007).
237 All subsampling was repeated 1000 times at regular circular area sizes varying from
238 0.5km² to 177km². Circular sample frames were increased in size by the addition of
239 500m to the circle's radius. The sub-samples were randomly located, using a random-
240 point generator in ArcGIS 9.2 (ESRI, Redlands, California, USA). Only sampling
241 frames containing a movement and completely contained within the study area were
242 used to derive movement statistics. All movement distances >0 km (i.e. not recaptures
243 at the same sett) were included in these statistics. Similarly, only movements
244 completed within sample frames were used to generate movement statistics. We
245 calculated the mean, median, and maximum movement lengths per sub-sampled study
246 area. In addition, we calculated movement statistics for the whole study area
247 (755km²). Finally, we used all movement data available, including data from marked
248 badgers recovered outside the study area (n = 3) to assess the potential largest scale
249 movements within the region.

250 The movement data from the subsampling study were modelled in a regression model
251 relating movement distance (D) to the sub-sample area size (\log_e transformed) and
252 number of movements recorded per sub-sample. Separate models were constructed
253 using all data, and for maximum D only. Regression models were assessed for
254 linearity, normality of residuals, multicollinearity and heteroscedasticity (see below;
255 Dohoo et al. 2009). Asymptotes were estimated from the predicted values from these
256 models and related to sample frame area sizes.

257 Dispersal kernel

258 Dispersal kernels measure the frequency distribution of movements within a
259 population by fitting mathematical forms (kernels) to the empirical data (Nathan et al.
260 2012). Derivations from these forms allow for the estimation of the expected
261 frequency of movement distances within a population (Baguette 2003; Fric and
262 Konvicka 2007). We use a broad definition of dispersal to generate dispersal kernels,
263 as being the “movement of an individual away from its source” (Nathan et al. 2003),
264 in our case from the sett of capture. However, we restricted the dispersal kernel
265 analysis to only movements $>1\text{km}$ (i.e. we invoked a threshold; Calsbeek 2009).
266 Movements $<1\text{km}$ are more likely representative of within territory movements, as the
267 mean and median nearest-neighbour distances between main setts within the study
268 area were 841m and 802m respectively (for all setts including non-main setts: mean =
269 367m; median = 268m). These movements were considered within ‘patch’
270 movements (*sensu* Baguette 2003), meaning our approach is similar to those taken
271 during metapopulation dispersal studies (e.g. Baguette, 2003; Calsbeek 2009).

272 We investigated the dispersal kernels of badgers in this population using two
273 functions: inverse power function (IPF) and negative exponential function (NEF).

274 Over twenty different movement kernel forms have been described (Hui et al. 2012;
275 Nathan et al. 2012), but these two forms have been popular and used in a number of
276 different systems (Baguette 2003; Fric and Konvicka 2007; Hui et al. 2012; Nathan et
277 al. 2012). Linear models (IPF vs. NEF) were compared using the Akaike's
278 Information Criterion (AICc) following Hui et al. (2012). We considered the best
279 fitting dispersal kernel to be fat-tailed if: *i.* the probability of long-distance
280 movements exceeded the predictions of a negative exponential distribution (Paradis et
281 al. 2002), *ii.* exponent β (n) value from the IPF was $0 < \beta < 2$ (Hui et al. 2012). We
282 assessed if there were sex related differences in frequency of badger movements
283 $> 1\text{km}$ in our study population by comparing IPF and NEF dispersal kernels for both
284 sexes. Separate models were run for both kernel types and the estimated β s and their
285 95% confidence intervals (CI) compared to see if there was an overlap as a heuristic
286 measure of significant dispersal difference. A comparison of regression slopes was
287 undertaken using analysis of covariance (ANCOVA) with length as the covariate and
288 gender as a factor variable. Finally, a two-sample Kolmogorov-Smirnov (KS) test was
289 performed on the kernels generated from data from female and male badgers (Hui et
290 al. 2012). The critical value for rejecting the null hypothesis (that the kernels derive
291 from the same distribution) being $p < 0.05$.

292 Investigating the relationship between density, study scale and LDDs

293 There may be an underlying relationship between LDDs and estimated local
294 population density (e.g. Matthysen (2005)). Such a relationship would confound the
295 relationship between study spatial-scale and LDDs. To investigate the relationship
296 between estimates of local density, study spatial-scale and the maximum distance
297 recorded during badger studies, a literature search was undertaken to gather all

298 available data on European badger populations where maximum D and density was
299 recorded. Multivariable linear regression models were built to evaluate the
300 relationships between maximum D and spatial-scale of the study (area: km^2) and
301 estimated density (badgers. km^{-2}). Models were repeated using maximum, minimum
302 and mean reported density from the respective study populations. Assumptions of the
303 linear models were assessed including: linearity between outcome and independent
304 variables (lowess smoothed curve), normality of residuals (visual inspection) and
305 homoscedasticity (Cook-Weisberg test) (Dohoo et al. 2009). To meet these
306 assumptions area was \log_e transformed. Multicollinearity was assessed by the
307 Variance Inflation Factor. All modelling was conducted using Stata[®] 11 (StataCorp.
308 2009. Stata Statistical Software: Release 11. College Station, TX, USA.).

309 **Results**

310 In total, 1,935 capture events were recorded with 963 individual badgers identified
311 during the study period. Badgers within the study population exhibited sett fidelity,
312 with a slight majority of recapture events (52%) being at the same sett as the previous
313 capture. Of the badgers that moved, the movement frequency distribution was highly
314 skewed with 43% of movements ($n = 204$) being ≤ 1 km.

315 Using all movements within the study area (755km^2 ; presented in Fig. 1), the mean
316 movement distance was 1.67km; the inclusion of recoveries ($n = 3$) of marked
317 badgers from outside the study area increased the mean to 1.72km. There was no
318 difference in the median movement length whether or not badgers recovered from
319 outside the study area were included in the analysis (both medians = 1.19km). The
320 greater mean length including recoveries from outside the study area was due to one
321 exceptionally long movement of 22.08km.

322 **Dispersal Kernel**

323 Overall there were 270 movements greater than 1km recorded during the study, which
324 were used to derive dispersal kernels. Of these, the mean and 95%ile attempted
325 dispersal distance were 2.61 km and 7.28 km, respectively. The distribution was
326 highly leptokurtic (kurtosis = 23.99; variance = 4.35). The kernel for these
327 movements was best represented by an IPF (Fig. 2). The IPF model had a better fit
328 and smaller AIC (IPF: $R^2=0.87$; AIC=199.04) than the NEF model (NEF: $F_{1, 268} =$
329 380.56 ; $p < 0.0001$; $R^2=0.59$; AIC= 554.54). The β of the IPF regression model was
330 < 2 , indicating that the expected dispersal distance is unbounded. The NEF severely
331 underestimated the fraction of movements at distances 1–2km ($\Delta_{\text{prop}} = -0.29$), and

332 overestimated the fraction of movements at distances between 2km and 10km (mean
333 $\Delta_{prop} = 0.024$; Fig. 2). The NEF underestimated the probability of LDD attempts at
334 distances ≥ 10 km in comparison with the IPF model. The IPF estimated population
335 probabilities of movement (fraction) of 0.011, 0.005 and 0.003 for dispersal distances
336 of 10km, 15km and 20km, respectively over the period of the study (Table 1).

337 There was a higher frequency of male movements ≥ 1 km (68%; $n=184$) than female
338 movements (32%; $n=86$). IPF models indicated shallower estimated slopes of decline
339 (β) for female badgers than male badgers (Table 1; Fig. 3). The 95% CI values did not
340 overlap when kernel models were estimated separately (upper 95% CI for female: -
341 1.599; lower 95% CI for male: -1.741). An ANCOVA indicated that this difference
342 between slopes was significant ($P < 0.001$). Similar results were found with NEF
343 models. The Kolmogorov–Smirnov test suggested that the movement distributions
344 were significantly different between the sexes ($D_f = 0.176$; $P = 0.039$). The 95%ile
345 dispersal distance for females was 9.44km; whereas for males the 95%ile was
346 4.37km. These results indicate at movement distances ≥ 1 km that *i*) male badgers
347 move more frequently than female badgers, *ii*) females make comparatively more
348 long-distance movements, as a proportion of movements recorded, than male badgers.

349 Sampling scale

350 Movement distances (D) increased significantly with increasing log-area size ($\beta =$
351 0.197 ; $t = 12.83$; $P < 0.001$) and were also positively associated with the number of
352 movements ($\beta = 0.001$; $t = 3.85$; $P < 0.001$) detected per sample. Log-area was
353 positively associated with the maximum distance (max. D) moved ($\beta = 1.987$; $t =$
354 13.73 ; $P < 0.001$), but not the number of movements ($\beta = -0.005$; $t = -1.76$; $P = 0.107$)
355 detected per sample. Using circle sampling frames of increasing size, the mean and

356 maximum movement distances increased logarithmically before approaching an
357 asymptote at spatial-scales greater than 80 km² in size (Fig. 4A and 4B; model
358 predicted asymptote sample areas size for mean movements: 132.7 km²; maximum
359 movement: >176.7 km²). The median movement distance increased logarithmically
360 up to 20km², and then increased very gradually thereafter up to 80 km² (Fig. 4A).
361 Many of the longest distance displacements would not have been recorded at scales
362 below this (80 km²) spatial extent (Fig. 4B).

363 Multi-population analysis: scale, density and LDDs

364 In total, data from 15 badger populations were gathered from the literature (including
365 data from the present study; Table 2). The data met the assumptions of the linear
366 model with linearity between outcome and dependent variables (lowess curve),
367 normally distributed residuals and no evidence of heteroscedasticity (all models
368 Cook-Weisberg test: $p > 0.42$). VIF was very low (1.16 - 1.17), despite there being a
369 moderate negative correlation between dependent variables ($r = -0.38$). Overall, the
370 model using mean density as a predictor significantly explained 71% of the variation
371 in the dataset ($n = 15$; $F_{2, 12} = 14.79$; $P < 0.001$; $r^2 = 0.71$). Controlling for mean
372 estimated density, there remained a significant positive relationship between study
373 area size and max D ($\beta = 0.02$; $P = 0.003$). Mean density was a marginally significant
374 predictor and was negatively associated with max D ($\beta = -0.22$; $P = 0.044$). Similar
375 model results were found when minimum density (Area: $\beta = 0.02$; $P = 0.003$; Min.
376 density: $\beta = -0.36$; $P = 0.054$) and maximum density (Area: $\beta = 0.02$; $P = 0.003$; Max.
377 density: $\beta = -0.17$; $P = 0.042$) were used as dependent variables in separate models.

378

379 Figure 5 demonstrates the predicted relationship between maximum D and study area
380 size, while adjusting for estimated mean population density (marginal mean effect).
381 Studies far below the model predicted regression line have shorter reported maximum
382 D than would be expected given study area size and density (Oxford, Gloucestershire
383 2, Brighton and Offaly (see Table 2)). These studies did not include chance recoveries
384 of animals found outside of the study areas. Studies above the regression line tended
385 to include chance recoveries from outside of the study area (Cork, Gloucestershire 1,
386 Bristol and Kilkenny, but not Białowieża).

387 **Discussion**

388 European badgers are territorial across much of their geographical range, with many
389 movements occurring within the boundaries of their social group's territory (e.g.
390 Rogers et al. 1998). The population studied here exhibited this general trend, with the
391 majority of badgers being recaptured at the same sett where they had been captured
392 previously. When badgers were encountered at a different location, 43% represented
393 movements of ≤ 1 km in length (which are likely within group movements in this
394 population, but could represent intergroup movements in higher density populations).
395 These findings are broadly consistent with previous research on badgers' populations
396 at a range of densities. However, the recording of long-distance movements within
397 this population, and a quantification of the frequency of such movements, is novel and
398 can be attributed to the unprecedented scale of this study.

399 We found that there was a strong relationship between metrics of badger movement
400 (mean, median and maximum D) and the spatial-scale of the subsampled study area
401 within our study. The size of the subsampled area had a particular impact on the
402 distribution of distances moved, fundamentally truncating the movement distribution.
403 According to our data, in order to adequately characterize badger movement
404 distributions, study areas of ≥ 80 km² may represent appropriate scales for similar
405 density populations. Currently, many studies of badger movements in Britain and
406 Ireland are undertaken at scales of < 20 km² (Table 2). In continental Europe, the
407 spatial-scale of badger movement studies has been often greater than 80 km².
408 Nonetheless, for logistical reasons, these continental studies can be compromised by
409 small sample sizes (mean number of badgers tracked: 12.5; range: 7-24; data from
410 Table 2). The probability of recording LDDs with such small sample sizes is low.

411 A meta-analysis of the available data in the literature on badger movements indicated
412 that there is a significant relationship between the greatest movement distances
413 recorded (max. D) and the spatial-scale of the study (Table 2). Though this
414 relationship is confounded by the estimated density of the populations under study
415 because there is a tendency ($P = 0.042-0.054$) for longer distance movements to be
416 recorded in lower density populations. This pattern may result from an interaction
417 between population ‘packing’, increasing the resistance to movement between groups
418 (higher ‘social viscosity’) due to population density, and also due to socio-spatial
419 distribution where lower density populations have larger distances to travel between
420 groups (Ronce 2007). Often where long-distance movements have been recorded in
421 higher density populations, they are a result of chance findings (recovery) of marked
422 badgers outside the study area (Table 2). In low-density populations, badgers are
423 capable of moving large distances in relatively short periods of time (maximum 6.9-
424 17.5 km night⁻¹; see references in Table 2); but typically these distances are travelled
425 tortuously and almost exclusively within their home range (Loureiro et al. 2007). It
426 should be noted that, due to the nature of the data collection, many movements made
427 at shorter temporal scales may have been missed during the present study. However,
428 at the spatial scale of the study, the relative frequency of movements across the
429 distribution should not be significantly biased, especially estimates from the IPF
430 which is invariant to marking frequency (Fric and Konvicka 2007). During our study,
431 we recorded a movement by a female badger of 22.1km; to the best of our knowledge,
432 this is the longest displacement recorded for a badger in the British Isles.

433 Sex-biased dispersal is common in the animal kingdom (Greenwood 1980). In birds
434 for example, the tendency is for females to disperse more frequently than males. In
435 mammals generally the opposite is true (i.e. higher frequency of male dispersal)

436 (Greenwood 1980), and there is also a tendency for males to travel further (Lawson-
437 Handley and Perrin, 2007). In mustelids, clear trends have not emerged with dispersal
438 frequency and distances being found to be male, female or non-biased amongst
439 species (e.g. Blundell et al. 2002; Dalerum et al. 2007) There has been variable
440 evidence of sex biased dispersal in badgers specifically in the literature (Roper et al.
441 2003). Some studies found evidence of male-biased dispersal (e.g. Rogers et al.
442 1998), while other data suggest female-biased dispersal (e.g. Woodroffe et al. 1993).

443 The literature on badger dispersal has been biased towards very high-density
444 populations (Frantz et al. 2009). An exception to this used genetic methods to
445 compare a high-density (up to 25 km⁻²) English population with a lower-density
446 (~1km⁻²) Swiss population (Frantz et al. 2009). That study reported badgers
447 dispersing greater distances in the lower-density Swiss population than the higher-
448 density English population. Furthermore, dispersal was female biased in the lower
449 density Swiss population whereas no consistent trend was found for a sex bias in the
450 English dataset. In our study population, female badgers had higher probability of
451 moving longer distances than male badgers, though there was higher frequency of
452 male movements recorded. This may suggest that sex-biased movement distances in
453 badgers is a scale-dependent phenomenon (biased toward males at intermediate scales
454 and females at larger scales), as found in other animals systems (e.g. common vole
455 *Microtus arvalis*, Gauffre et al. 2009). This hypothesis would help to explain the
456 apparent discordancy within the literature, but further research is needed to test this
457 (or alternate) hypothesis.

458 In the dispersal kernel analyses, we limited the dataset to badger movements ≥ 1 km in
459 length. These dispersals may represent either permanent or temporary dispersal

460 movements away from a home territory, with both being potentially biologically
461 meaningful. Temporary visits to adjacent territories have been shown to result in
462 successful breeding (Dugdale et al. 2007), and have been correlated with tuberculosis
463 disease status (Rogers et al. 1998; Vincente et al. 2007). Permanent movements can
464 result in greater likelihood of breeding success for dispersing badgers (Woodroffe et
465 al. 1993; Macdonald et al. 2008) and long-distance dispersals are known to contribute
466 to the spread and maintenance of bTB in other model systems (e.g. brushtail possum
467 *Trichosurus vulpecula*; Ramsey and Efford 2010).

468 Our data have implications for disease transmission, as long-distance movement made
469 by individuals could result in the transmission of disease across landscapes. For
470 example, dispersing badgers can accumulate more bite wounds (Macdonald et al.
471 2008) than badgers that stay within their social group, and this is a risk-factor for bTB
472 (Murphy et al. 2010). Previous work has found multiple bTB strains within setts, and
473 some strains being different to those of the local cattle population (Olea-Popelka et al.
474 2005; Kelly et al. 2010; Woodroffe et al. 2005b) with strains geographically
475 clustering at large scales (>6km in Ireland; Olea-Popelka et al. 2005; Kelly et al.
476 2010). This led to speculation that long-distance badger movements could have been
477 involved in the spatial spread of bTB strains across landscapes (Olea-Popelka et al.
478 2005), but until now there were no data to support large-scale movements
479 interconnecting badger populations (Fig. 1). Simulation modelling suggests that
480 increasing the frequency or length of dispersal attempts can have effects on the spread
481 and persistence of bTB in badger populations (e.g. Hardstaff et al. 2012). In lower
482 density populations, for example, infection may be seeded, or disease prevalence
483 maintained, in relatively isolated populations from dispersing badgers (Hardstaff et al.
484 2012). Currently, the test status of the badgers within this population is unknown, thus

485 the epidemiological significance of badger LDDs is still speculative. However, this
486 speculation must be considered against a backdrop of high bTB badger prevalence in
487 Ireland (36%; Murphy et al. 2010) and parts of Britain (35-53%; Carter et al. 2012).

488 When designing vaccination or culling field trials with different treatments, it is
489 important to ensure that the study sites are spatially independent (Bourne et al. 2007;
490 Pech et al. 2010). Conversely, it is desirable for study sites to be as geographically
491 similar as possible (Bourne et al. 2007). Given our findings, we would expect that 5%
492 of badger dispersal attempts in this population would be at distances of >7.3km over a
493 four-year study. This would indicate that, in the absence of physical movement
494 barriers, buffers of ≥ 7.3 km may be needed to restrict inward dispersal and maintain
495 site independence with a high degree of confidence. Despite this, the probability
496 threshold chosen would depend on many other (including socio-economic) factors
497 (Pech et al. 2010).

498 Our study highlights the difficulty in studying the ‘tail’ of the dispersal distribution of
499 mammals – even in a species that exhibits natal philopatry and general low dispersal
500 probabilities (Woodroffe et al. 1993). Future studies of badger dispersal will require
501 large scales and long time periods if an Eulerian approach is used (i.e. the use of
502 marked animals; Nathan et al. 2003). Alternatively, for Lagrangian methods (i.e. the
503 use of tracked animals; Nathan et al. 2003) there is a need to increase sample size and
504 temporal scales, but also the ability to track animals once they move outside the
505 boundary of a study site (Hebblewhite & Haydon 2010). Development of GPS/GSM
506 technology may improve such tracking studies as costs decrease permitting more
507 animals to be tracked over greater spatial-scales (Hebblewhite & Haydon 2010). Until
508 then, our results highlight the importance of spatial-scale in the study of a medium-

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509 sized mammal movements, especially one which is a host for an economically
510 significant disease of domestic animals.

511

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519

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703 **Table 1.** Results of fitting inverse power functions (IPF) and negative exponential functions (NEF) to badger (*Meles meles*) movement data. β is
 704 the slope of the fitted linear regression; all regression slopes were significant at $p < 0.001$. *Prop* represents the model-estimated probability of
 705 movement at 10km, 15km, 20km over the study period.

Data	Kernel	β	Log-	AIC	Δ AIC	r^2	Prop		
		(95% CI)	likelihood				10km	15km	20km
Male (n = 184)	NEF	-0.354 (-0.398 – -0.311)	-173.110	350.22	-	0.58	0.0111	0.0019	0.0003
	IPF	-1.844 (-1.947 – -1.741)	-64.598	133.20	-217.02	0.87	0.0083	0.0039	0.0023
Female (n = 86)	NEF	-0.249 (-0.293 – -0.205)	-93.306	190.61	-	0.60	0.0204	0.0059	0.0017
	IPF	-1.480 (-1.599 – -1.362)	-41.429	86.86	-103.75	0.88	0.0130	0.0071	0.0047
All (n = 270)	NEF	-0.299 (-0.329 – -0.268)	-275.269	554.54	-	0.59	0.0162	0.0037	0.0008
	IPF	-1.676 (-1.754 – -1.598)	-120.348	244.69	-309.84	0.87	0.0106	0.0054	0.0033

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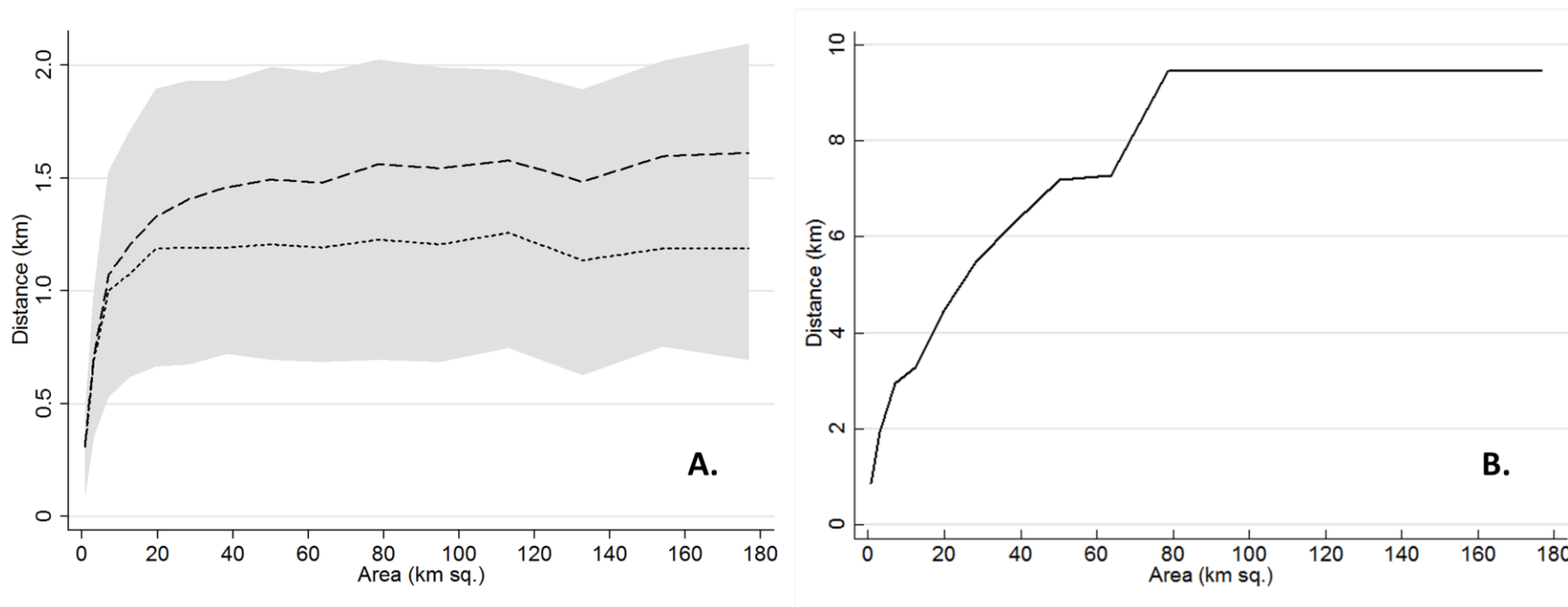
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710 **Table 2.** Badger movements (*D*) recorded during mark-recapture (MRR) and tracking studies (T) from 14 populations. Tracking data allows for
 711 fine temporal resolution of movements. MRR movements are of coarser temporal scale, where movements may have occurred at times usually
 712 >30 days. MMR are the minimum distance moved, as they are measured as straight lines between capture points. Sample size = number tracked.
 713

Type	Country	Max. <i>D</i> (km)	Sample size	Density (Adults Km ⁻²)	Study area (km ²)	Reference (Supplementary material)
MRR	England (Brighton)	3.3 (recovery) ²		16.9-35.3	2	S1
MRR	England (Oxford)	1.7 ³		15.0-38.0	4.2	S2;S3
MRR	England (Bristol)	7.8 (recovery) ⁴		4.4-7.5	5.5	S4;S5
MRR	England (Gloucestershire 1)	8.3 (recovery) ⁴		7.8-15.1	9	S5;S6
MRR	England (Gloucestershire 2)	3.0		7.8-25.3	11	S6;S7
T	Ireland (Cork)	11.0 (recovery) ⁴	12	0.5-2.9	14	S8;S9
T	Denmark	6.9	10	1.5	15	S10
MRR ¹	Ireland (Offaly)	3.1		3.2-5.9	16	S11
T	Portugal	9.2	9	0.4-0.5	66	S12;S13
T	Switzerland	7.0 (recovery) ⁴	14	1	74	S14
T	Poland (Rogów)	8.1	8	0.8-1.4	89	S15;S16
T	Poland (Białowieża)	17.5	13	0.09-0.13	130	S17;S18
T	Spain	11.6	24	0.2-0.7	240	S19;S20
T	Belarus	9.1	7	0.09	330	S21

714 ¹ Using coloured-bait returns. ² Found dead inside study area. ³ Estimated from data presented in paper. ⁴ Found dead outside study area.



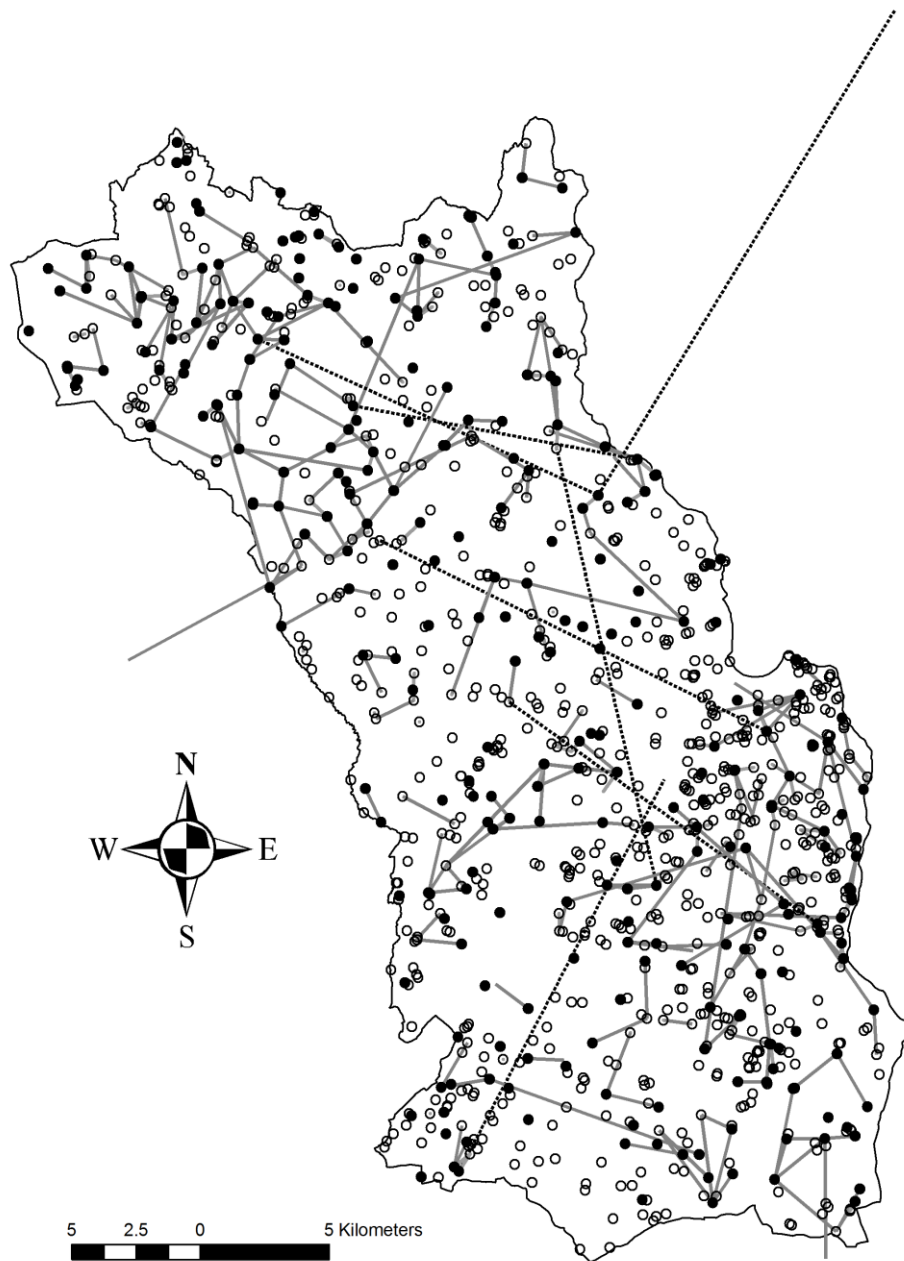
715

716 **Figure 4.** Subsampling (1000 samples) movements using circles of increasing radii. A. *Dashed line* represents the mean movement distance
717 recorded. *Dotted line* represents the median movement distance recorded. The *shaded area* represents the upper 75th and lower 25th percentile. B.
718 *Solid line* shows the relationship between the maximum recorded movement and area size.

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723 **Figure 1.** Recorded movements made by marked badgers in the Kilkenny study area.

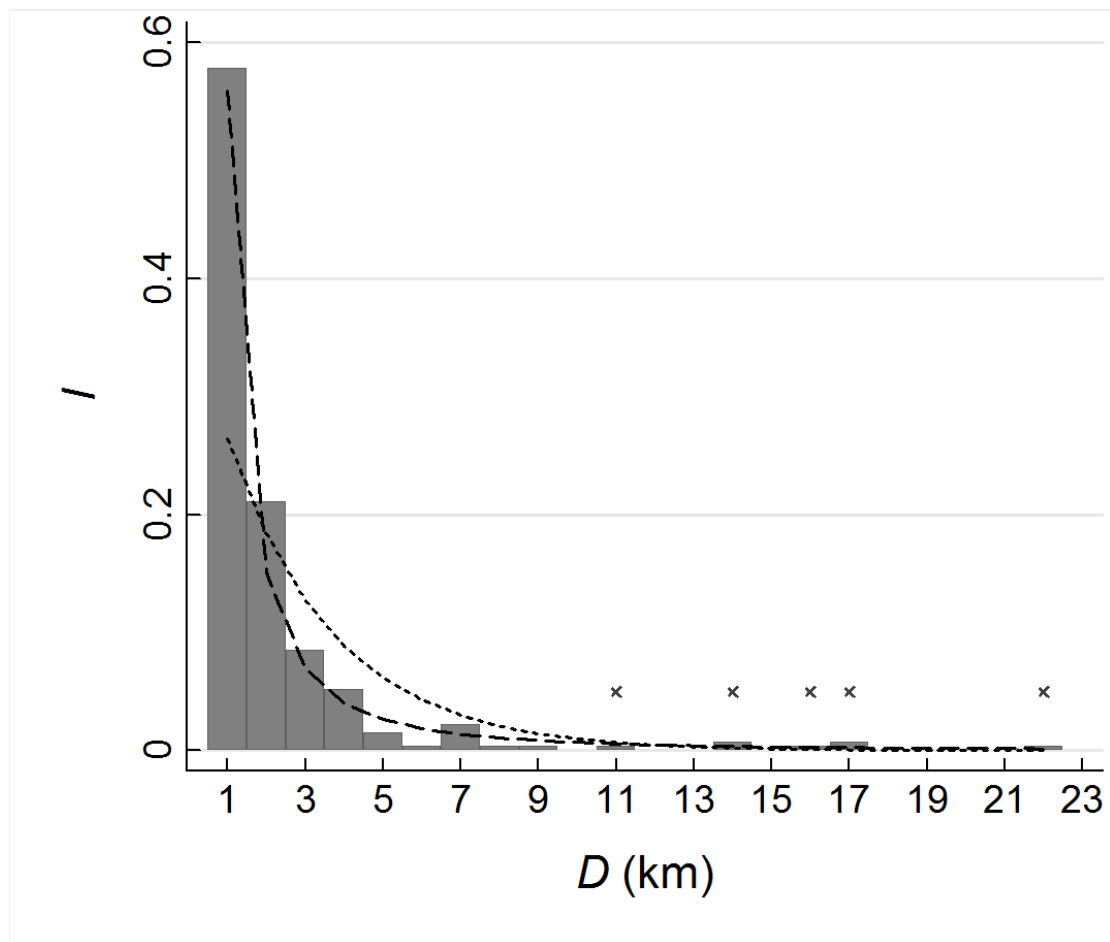
724 Black dots represent main setts; hollow dots are non-main setts. Solid lines:

725 movements <10km; Dotted lines: movements >10km.

726

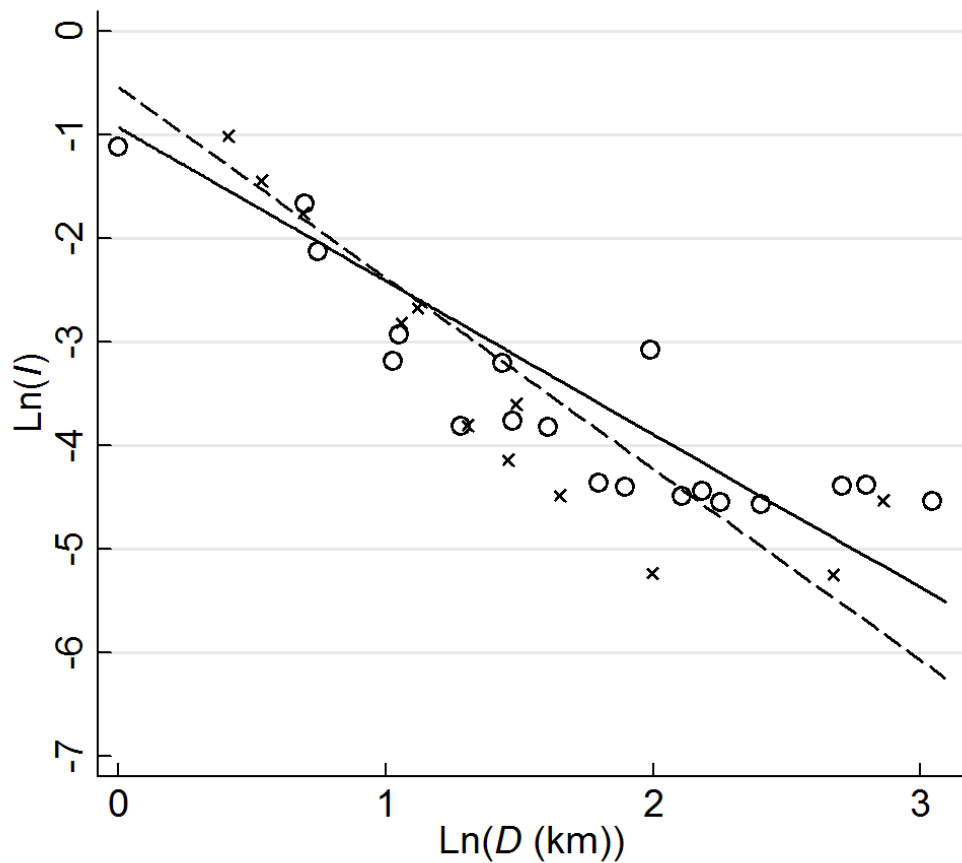
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730 **Figure 2.** Predicted inverse power function (IPF; *dashed line*) and the predicted
731 negative exponential function (NEF; *dotted line*) density distribution (*I*) in relation to
732 the observed proportion of movements (*D*) over 1km distance. Crosses denote bins
733 with observed long-distance movements.

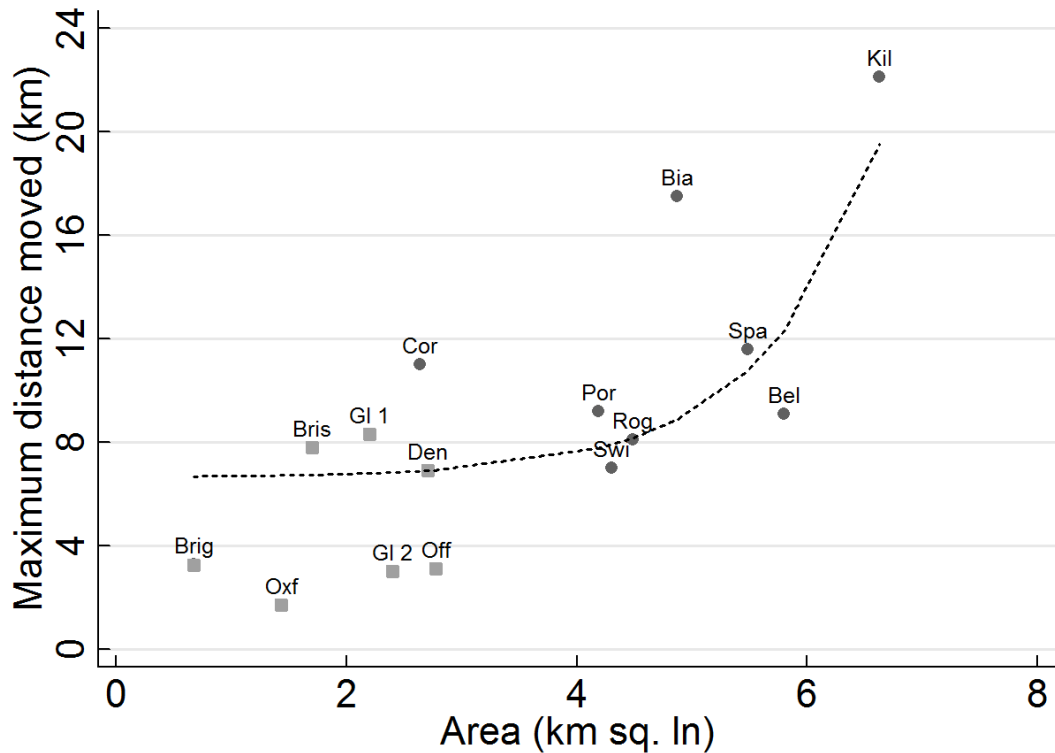


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735 **Figure 3.** Regression lines of the predicted inverse power function (IPF) for male
736 (*dashed line*) and female (*solid line*) badger movements. Dispersal kernels were
737 produced using distance classes, with all records within each class binned to the
738 movement distance (D). I is the probability density of movements to distance D .

739 Crosses = male; circles = female.

740



741

742 **Figure 5.** Linear regression line (dashed), adjusted by the mean marginal effect of
743 local density, of the predicted relationship between study area size (log km²) and
744 maximum distance moved as recorded during studies of 15 populations across
745 Western Europe. Squares represent populations with minimum densities of >1
746 badger.km⁻²; circles represent populations with minimum densities of ≤1 badger.km⁻².