

# Population-level zoogeomorphology: the case of the Eurasian badger (*Meles meles* L.).

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## ABSTRACT

The zoogeomorphological impact of burrowing animals varies in time and space as a result of the particular life-history traits of the organisms involved, the patchy distribution of habitat resources, and fluctuations in population size. Such ecological complexity presents a major challenge for biogeomorphologists wishing to upscale from individuals to populations.

Using a unique ecological dataset for Eurasian badgers (*Meles meles* L.) in Wytham Woods, Oxfordshire, UK, we show that direct zoogeomorphological impact (soil displacement during sett excavation) is constrained by fluctuations in overall population size. Modelled digging rates for individual badgers ( $0.19\text{--}4.51\text{ m}^3\text{ yr}^{-1}$ ) varied depending on the ecological function of the sett they are associated with, and we estimate that the whole population has displaced  $304\text{--}601 \pm 72\text{ m}^3$  of soil during the construction of 64 setts. This represents an overall excavation rate of  $6.7\text{--}19.4\text{ m}^3$  ( $6.0\text{--}17.5\text{ t}$ )  $\text{yr}^{-1}$  in sett areas, or  $1.42\text{--}4.12\text{ g m}^{-2}\text{ yr}^{-1}$  when averaged over the whole 424 ha woodland.

As well as direct soil displacement, badger digging exposes material that is initially susceptible to erosion by water relative to undisturbed, litter-covered soils. Over time, setts become stabilized, representing unique landforms that persist in the landscape for decades to centuries.

**KEY WORDS:** Burrowing, biogeomorphology, bioturbation, *Meles meles*, ecosystem engineering, Wytham Woods

## 29 **Introduction**

30 Many animals dig underground nests and burrows for refuge from predators and the  
31 provision of safe conditions for the birth and rearing of young (Kinlaw, 1999; Meadows,  
32 1991; Reichman & Smith, 1990; Whitford & Kay, 1999). Through these activities fossorial  
33 (burrowing) animals can displace and deposit large quantities of sediment ('spoil') at the  
34 surface in mounds or heaps. These conspicuous surface features have received sustained  
35 interest from geomorphologists wishing to quantify the impact of living organisms on the  
36 landscape (e.g., Viles, 1988; Butler, 1995).

37  
38 As well as direct spoil displacement, burrowing animals mix, aerate, and compact  
39 sediment (Hole, 1981). This bioturbation (or 'biopedturbation', Whitford & Kay, 1999)  
40 means that soil nutrient and organic content, water-holding capacity, infiltration and  
41 hydrological conductance, pH, color, texture, structure, and stability can all vary  
42 significantly when compared with undisturbed soils (Carlson & White, 1988; Eldridge,  
43 Koen, Killgore, Huang, & Whitford, 2012; Gabet, Reichman, & Seabloom, 2003; Garkaklis,  
44 Bradley, & Wooller, 2004; Wilkinson, Richards, & Humphreys, 2009). The consequent  
45 impacts of burrowing and digging on soil erodibility and sediment transport rates are of  
46 particular interest to geomorphologists (e.g., Black & Montgomery, 1991; Neave &  
47 Abrahams, 2001; Yoo, Amundson, Heimsath, & Dietrich, 2005).

48  
49 At the same time, burrowing animals are recognized as being ecologically important as  
50 ecosystem engineers (Jones, Lawton, & Shachak, 1994, 1997); the physical impacts of  
51 organisms (the primary focus for geomorphologists) often have additional consequences  
52 (feedbacks) for the distribution, interaction, survival, and evolutionary fitness of other  
53 organisms via the creation—and subsequent decay—of physical habitat resources  
54 (Corenblit et al., 2011; Cuddington, Byers, Wilson, & Hastings, 2007; Hastings et al., 2007;

55 Jones, 2012; Wright & Jones, 2006). In this respect, many studies have demonstrated the  
56 importance of burrowing and digging for nutrient cycling, seed dispersal, vegetation  
57 community dynamics, intra- and inter-species interactions, biodiversity, ecosystem  
58 resilience to environmental change, and habitat restoration and management (e.g., Byers  
59 et al., 2006; Eldridge, 2011; Eldridge et al., 2012; Eldridge, Whitford, & Duval, 2009;  
60 Fleming et al., 2014; Hansell, 1993; James, Eldridge, & Moseby, 2010; Kinlaw &  
61 Grasmueck, 2012; Maestre et al., 2012; Martin, 2003; Meadows & Meadows, 1991; Zaitlin  
62 & Hayashi, 2012).

63  
64 On-going integration of biogeomorphology and ecosystem engineering (e.g., Butler &  
65 Sawyer, 2012) is fuelling important conceptual debates about the significance of  
66 organisms' physical impacts at increasingly large spatial and temporal scales (e.g.,  
67 Corenblit, Gurnell, Steiger, & Tabacchi, 2008; Jones, 2012; Viles, 2012). A major  
68 challenge here is a general lack of suitable data to quantify animal impacts beyond the  
69 scale of individuals. This is critical, however, if the significance of the collective impacts of  
70 individuals (forming populations) and whole ecological communities are to be fully  
71 appreciated at a landscape scale (Coombes, in press; Dietrich & Perron, 2006; Naylor,  
72 Viles, & Carter, 2002; Reinhardt, Jermlin, Cardinale, Vanacker, & Wright, 2010).  
73 Recent work has demonstrated the potential for modelling to address these issues (e.g.,  
74 Gabet, Perron, & Johnson, 2014; Yoo et al., 2005), but the availability of suitable  
75 ecological data remains a major constraint.

76

77 **Badgers as geomorphic agents**

78 All ten species of badger dig and inhabit burrows (Long & Killingley, 1983). The Eurasian  
79 badger (*Meles meles* L.) is unique among these, however, in that it has evolved sociality  
80 and communal living in underground burrow systems, called setts (Kruuk, 1989). Eurasian

81 badgers live in defended territories as part of a social group, usually occupying one main  
82 sett and several smaller subsidiary setts ('outliers' or 'annexes') that have different  
83 functions including resting, winter sleeping, and breeding and rearing of cubs (Kaneko,  
84 Newman, Buesching, & Macdonald, 2010; Kruuk, 1978a, 1989; Neal, 1977; Roper, 1992a;  
85 Thornton, 1988). A single sett may be inhabited by up to 35 individuals at any one time  
86 (Woodroffe & Macdonald, 1993); however, the size of a sett is not related to the size of the  
87 social group it currently supports (Kruuk, 1978a; Neal, 1977) but is more a function of its  
88 use as a main or subsidiary sett, its age, the substrate it is dug in, and the life-history traits  
89 (including sex, fecundity, and sett fidelity) of all the occupants that have ever lived there  
90 (Dunwell & Killingley, 1969; Kruuk, 1989; Neal & Roper, 1991; Roper, 1992a; Stewart,  
91 Bonesi, & Macdonald, 1999).

92  
93 Internal sett architecture is highly variable (Roper, 1992b) but tunnels are typically dug in a  
94 zone that extends from the surface to 1.5–2 m vertical depth (Kaneko et al., 2010). When  
95 excavating tunnels, badgers loosen earth with the forelimbs before bringing the hind legs  
96 forward and backing out to push soil up to the surface, often kicking spoil clear of the  
97 burrow entrance in a downslope direction (Neal & Cheeseman, 1996). The progressive  
98 accumulation of spoil (across generations) forms surface mounds (Figure 1) reported to  
99 exceed 30–40 m<sup>3</sup> in volume in some cases, and which often coalesce to form larger  
100 surface features, hereafter referred to as 'sett surface complexes'. A similar process  
101 ('cannibalisation') has been reported for pocket gopher mounds (Gabet et al., 2014). Three  
102 to ten entrance holes is fairly typical for a main sett, although setts with almost 200  
103 entrances have been reported (Roper, 1992a, b). The re-excavation of old entrance holes,  
104 extension of existing tunnels, and excavation and connection of new chambers to the  
105 surface exposes sediment to surface processes in occupied areas. As well as digging to

construct burrows, badgers may dig shallow foraging pits (or ‘scrapes’, Wilkinson et al., 2009) when searching for earthworms and other foodstuffs (Kruuk, 1978b).

Despite a vast ecological literature on the burrowing behavior of this species, we are aware of only one study that has explicitly focused on the geomorphological significance of *M. meles* (Voslamber & Veen, 1985). The potential of Eurasian badgers as physical ecosystem engineers has too only been acknowledged relatively recently, in reference to soil nutrient dynamics and plant communities (Kurek, Kapusta, & Holeksa, 2014). Here, we use field observations alongside a multi-decadal dataset for a population of *M. meles* in Wytham Woods, Oxfordshire, UK, to: (1) evaluate the relationship between population dynamics and landscape-scale digging activity; (2) quantify the direct zoogeomorphological impacts of badgers at this site by estimating the volume of soil displaced during the construction of setts, and; (2) evaluate the indirect zoogeomorphological significance of badger burrowing by characterizing the erodibility of spoil material once deposited at the surface.

121

## 122 **Study site**

Wytham Woods (OS SP 462 080) occupy 424 ha of land 5 km north-west of the City of Oxford, UK (Figure 2). The woods lie over two outlying hills of the Cotswold Escarpment (Wytham Hill and Seacourt Hill) varying in altitude from 60–165 m above sea level (Macdonald, Newman, Dean, Buesching, & Johnson, 2004). Geology consists of Middle Jurassic Coral Rag topped with clayey soils from the Sherbourne and Morton series that rest on Lower Calcareous Grit sands. This characteristically orange-yellow sand encircles the two hills (Figure 2) and is the preferred digging medium for the badgers (Hofer, 1988; Kruuk, 1978a) (Figure 3a–b).

131

132 The Wytham badgers have been studied intensively since the 1970s (first described in  
133 detail by Kruuk, 1978a, b) and a comprehensive trapping program was initiated in 1987  
134 (four trappings per year) providing detailed life-history data for all individual badgers and  
135 setts (Macdonald & Newman, 2002; Macdonald, Newman, Nouvellet, & Buesching, 2009).  
136 Here we use data collected between 1987 and 2004 (a 17-year period). As of 2004, the  
137 population consisted of 213 badgers (190 adults), representing the highest density in the  
138 world (around 38 per km<sup>2</sup>). Setts had a density of about 70 per km<sup>2</sup>, consisting of 64  
139 named main setts (which we focus on in this study) and an additional 215 smaller digging  
140 sites, all organized into 24 independent social groups (Macdonald et al., 2004) (Figure 2).

141

## 142 **Methods**

### 143 **Population-level zoogeomorphology**

144 As a means of assessing relationships between population dynamics and direct  
145 zoogeomorphic activity (i.e., sett excavation), the years in which setts were first recorded  
146 were determined from annual survey records (from 1987 onwards). The number of newly  
147 constructed setts was then compared to annual population data from the trapping  
148 database (Department of Zoology, University of Oxford).

149

### 150 **Direct impacts: sett excavation volume**

151 The total volume of soil moved during excavation of all named setts ( $n = 64$ ) was  
152 estimated using two different modelling approaches, allowing for comparison between  
153 methods. First, predictive regression models were used to estimate sett subsurface  
154 volume from measurements of sett surface area made in the field. Second, 3D models of  
155 two sett surface complexes were used to derive 'average digging rates' for individual  
156 badgers, which were subsequently extrapolated for the whole population. Each approach  
157 is outlined, in turn, in the following sections.

158

159 *Method 1: Estimating excavated soil volume from sett surface area*

160 Around half of all named setts were located during summer 2005 ( $n = 29$ ) and their surface  
161 areas measured as the extent of existing mounds and spoil. Observations of the influence  
162 of setts on the local topography were also made. In order to derive surface area estimates  
163 for the remaining unvisited setts ( $n = 35$ ), a predictive model was constructed using a  
164 variety of ecological parameters (available for all setts) from the trapping database (Table  
165 1) and multiple regression. This 'area model' (eq. 1) had statistically significant predictive  
166 power for the surface area of visited setts ( $R^2 = 0.73$ ,  $p < 0.001$ ):

167 
$$A = 8.7a + 1.0X_{yr} + 15.5c - 7.2u - 20.7 \quad (\text{eq. 1})$$

168 where  $A$  = sett surface area ( $\text{m}^2$ ),  $a$  = sett age (years),  $X_{yr}$  = excavation years,  $c$  = sett  
169 fecundity (number of cubs), and  $u$  = unique residency (number of adults) (see Table 1 for  
170 full explanation of these parameters).

171

172 Surface area data (both measured and modelled) were then used to estimate the  
173 subsurface volume of setts using a simple 'volume model' (eq. 2). This model was derived  
174 from existing area/volume data for 19 manually excavated setts published in Roper  
175 (1992b). This model had a statistically significant predictive power for sett subsurface  
176 volume ( $R^2 = 0.87$ ,  $p < 0.001$ ):

177 
$$V = 0.03A - 0.14 \quad (\text{eq. 2})$$

178 where  $V$  = sett subsurface volume ( $\text{m}^3$ ) and  $A$  = minimum sett surface area ( $\text{m}^2$ ).

179

180 *Method 2: Estimating excavated soil volume from individual digging rates*

181 The second approach used to estimate soil displacement volumes involved calculation of  
182 an average 'per badger excavation rate' ( $e$ ), which was then extrapolated for all members  
183 of the population, using the following principles. First, the amount of material constituting a

184 sett surface complex was assumed to result from the cumulative actions of all individual  
 185 badgers that have ever been resident there, excluding cubs as they do not dig (Neal &  
 186 Cheeseman, 1996), thus:

$$187 \quad E = E_1 + E_2 + E_3 \dots E_n \quad (\text{eq. 3})$$

188 where  $E$  = total sett excavation volume,  $E_1$  = excavation by badger 1,  $E_2$  = excavation by  
 189 badger 2, etc. Second, the number of years each adult badger has been resident at a sett  
 190 was used to define the potential number of 'excavation years' it has contributed to its  
 191 construction:

$$192 \quad E_n = e_n r_n \quad (\text{eq. 4})$$

193 where  $E_n$  = total soil excavated by individual  $n$ ,  $e_n$  = annual excavation by badger  $n$ , and  $r_n$   
 194 = residency of individual  $n$  at a sett (in years). Thus, the total number of 'excavation years'  
 195 ( $X_{yr}$ ) contributing to the construction of any sett can be defined as the cumulative total of  
 196 the residency (in years) of all adult badgers that have ever lived there, thus:

$$197 \quad X_{yr} = \sum_n r_n \quad (\text{eq. 5})$$

198 Note that  $X_{yr}$  will always be greater than the age of a sett where occupancy has been  
 199 greater than 1, as the model assumes all resident adult badgers contribute to digging.  
 200 Finally, assuming that individuals dig at a constant rate (see discussion), the total  
 201 excavated volume of any sett ( $E$ ) is estimated as a product of the total excavation years  
 202 ( $X_{yr}$ , eq. 5) and the average badger excavation rate ( $e$ ), thus:

$$203 \quad E = e X_{yr} \quad (\text{eq. 6})$$

204 In order to determine  $E$  for all main setts (using eq. 6), the number of excavation years  
 205 ( $X_{yr}$ ) was determined in each case from the trapping database (using eq. 5), and  
 206 representative values of  $e$  were calculated using the rearranged formula:

$$207 \quad e = \frac{E}{X_{yr}} \quad (\text{eq. 7})$$



208 where  $E$  was determined for two different sett complexes using topographic field surveys  
209 and 3-dimensional surface models, outlined below. An excavation volume ( $E$ ) for all 64  
210 named setts was then estimated (eq. 6) using the calculated values of  $e$  for the two  
211 reconstructed setts. This approach is unique in accounting for potential differences in the  
212 contribution of individuals to digging occurring as a function of residency time—an  
213 important consideration for bioconstructions built by social groups and successive  
214 generations of individuals.

215

216 For the 3D reconstructions, ‘Pasticks Outlier’ (PO) and ‘Mac Bracken’ (MB) setts were  
217 chosen for being in contrasting areas of the woods (Figure 2), having easy access, and  
218 being of known age (PO = 10 years, MB = 12 years). In both cases, relative spot-heights  
219 over the sett surface were calculated in a grid (1 m<sup>2</sup> resolution) using ranging poles and a  
220 clinometer. Relative spatial reference coordinates and calculated spot heights were then  
221 imported into GIS software (ArcMap) in XYZ format and Triangulated Irregular Network  
222 models (TINs) generated using 0.1 m interpolated contours. To calculate the excavation  
223 volume ( $E$ ) of both setts (to be used in eq. 7), all positive and negative elevation change  
224 components in the models relative to a ‘pre-disturbance’ plane (constructed from surveyed  
225 edge-points) were summed using cut-fill analysis within ArcMap Spatial Analyst.

226

227 **Indirect impacts: sett surface cover and spoil erodibility**

228 *Surface cover*

229 Percent cover ( $\pm 5\%$ ) of bare soil, vegetation, litter, and stones was estimated for four  
230 different patches on and around sett complexes (spoil mound tops, mound flanks, inter-  
231 mound areas, and control areas). Measurements were made across two main setts for  
232 comparison (Mac Bracken and The Mount, chosen mainly for access) in 20 quadrats (1  
233 m<sup>2</sup>) per patch. Data were compared using ANOVA to determine whether cover type varied

234 as a function of patch type. 'Patch' was a fixed factor (four levels) and 'cover type' was  
235 nested within 'patch' (three levels; stone cover data were excluded due to a high  
236 proportion of zero values). Data heteroscedasticity was corrected for using square-root  
237 data transformation.

238

#### 239 *Soil properties*

240 As a comparative measure of the resistance of sett surfaces and control soils to erosion by  
241 water and wind, penetration resistance (unconfined strength) was determined using a  
242 hand-held penetrometer at three setts (The Mount, Radbrook Common Outlier, and Mac  
243 Bracken). The force required ( $\text{kg cm}^{-2}$ ) to insert the probe to a depth of 5 cm was  
244 measured 30 times in four patches (fresh spoil, older mound flanks, badger paths used to  
245 reach foraging grounds, and control areas). Data were square-root transformed and  
246 compared using a one-way ANOVA (four levels of patch type).

247

248 Water Drop Penetration Time (WDPT) was also determined as a measure of soil surface  
249 tension and hydrophobicity (Doerr, 1998). For this, fifteen drops of distilled water were  
250 applied to levelled surfaces of air-dried soil samples collected from different sett patches  
251 (fresh spoil, crusted spoil, the flanks and bases of older mounds, and adjacent control  
252 areas). The time taken for droplets to fully infiltrate was then recorded. Wet and dry  
253 aggregate stability were also determined by carefully submerging individual aggregates (1  
254 cm in diameter) in distilled water and recording the time taken for partial and complete  
255 breakdown. Finally, composition and grain size analyses were undertaken for surface soil  
256 samples (all < 5 cm depth,  $n = 5$ ) from different sett patches (fresh spoil, crusted spoil,  
257 mound flank, mound base, and control areas) following standard wet and dry sieving  
258 techniques. Fine soil fractions were analyzed using laser granulometry.

259

## 260 **Results and Discussion**

### 261 **Population-level zoogeomorphology**

262 The badger population in Wytham Woods has shown distinct periods of growth and  
263 decline; the population tripled between 1987 and 1996, declined in the late 1990s, followed  
264 by a period of further growth (Macdonald & Newman, 2002; Macdonald et al., 2009). More  
265 recent trends have been related to climatic variability, most notably changes in rainfall  
266 and its impact on the availability of earthworms—the favored food stuff for the Wytham  
267 population (Macdonald et al., 2010; Nouvellet, Newman, Buesching, & Macdonald, 2013;  
268 Noonan et al., 2014).

269  
270 Figure 4 illustrates a clear relationship between minimum population size (number of  
271 unique badgers trapped each year) and the number of newly dug setts between 1987 and  
272 2004. Over this period the strongest correlation is achieved factoring in a 3-year lag  
273 between population size and sett establishment ( $R^2 = 0.67$ ,  $p = 0.006$ ). A similar  
274 relationship was reported by Macdonald & Newman (2002) for the period between 1987  
275 and 1996. Macdonald et al. (2004) also note that a peak in badger numbers occurred six  
276 years before a proliferation of new setts being excavated. This lag may reflect the time  
277 taken for cub cohorts to reach adulthood (and thus able to contribute to sett excavation) or  
278 the time required for the complex re-organization of social groups that precedes the  
279 establishment of new clans and setts (Macdonald et al., 2004).

280  
281 It follows that long-term population trends will be reflected in a non-uniform rate of soil  
282 displacement by badgers (in terms of sett excavation, and possibly population-scale  
283 foraging effort), and that factors affecting future population size will have subsequent  
284 (lagged) implications for soil displacement and topographic change. This includes climate  
285 change, the zoogeomorphological (and broader biogeomorphological) implications of

286 which remain understudied (see Butler, 2012). For many burrowing species, changes in  
287 climate and weather patterns are likely to have major ecological consequences for  
288 resource-dependent populations. For example, climate-driven changes in food availability  
289 are likely to have zoogeomorphological and well as ecological consequences by affecting  
290 the spatial density, temporal frequency, and intensity of foraging activity, and the number  
291 of individuals engaged in digging activity (e.g., Garkaklis et al., 2004; Hall & Lamont, 2003;  
292 Johnson, Jetz, & Macdonald, 2002; Macdonald & Newman, 2002; Macdonald et al., 2004;  
293 Nouvellet et al., 2013; Yair & Rutin, 1981). The Wytham badgers represent one of the first  
294 examples to clearly demonstrate the importance of population dynamics in driving  
295 zoogeomorphological activity at the local and landscape scale, over a decadal timescale.

296

297 **Direct zoogeomorphological impacts of badgers**

298 *Setts as bioconstructions*

299 Setts are distinctive bioconstructions in Wytham Woods. Whilst they vary greatly in lateral  
300 and vertical extent, Eurasian badger setts have significantly altered local topography. The  
301 height of sett mounds varied in the order of 0.2–2 m above the local topographic surface  
302 depending on sett age, underlying slope angle, position on slopes, and the presence of  
303 obstructions such as trees (Table 2). Sett dimensions are therefore comparable with  
304 landforms created by other noted fossorial mammals, including gopher mounds and  
305 wombat warrens (compared in Table 3).

306

307 In the steeper northern part of the woods, badgers have dug perpendicularly into slopes  
308 (to reach the looser grit sand layer) resulting in characteristic stepped profiles following the  
309 downslope movement of spoil. Similar stepped topography has been reported for gophers  
310 (Thorn, 1978) and rabbits (Rutin, 1992). In the flatter southern areas of the woods,  
311 badgers dig vertically into the ground to reach the sand layer, giving more characteristic

312 'doughnut' morphology to mounds. Collapsed burrows and entrances were noticeable  
313 features of some setts (Figure 3c), creating localized surface depressions (typically < 0.5  
314 m depth) that had been re-excavated in some instances. Similar topographic features have  
315 also been reported for rabbit warrens (Eldridge & Myers, 2001), grizzly bear dens (Butler,  
316 1992, 1995), and puffin burrows (Furness, 1991).

317

#### 318 *Excavated soil volume 1: estimates from sett surface area*

319 The combined surface area of 29 visited setts was 5,832 m<sup>2</sup>. Doubling this gives a crude  
320 estimate of the total area modified by badgers during the construction of all 64 named  
321 setts (11,664 m<sup>2</sup>). This is equivalent to just 28 m<sup>2</sup> ha<sup>-1</sup> across the whole woodland site and  
322 illustrates the highly non-uniform spatial distribution of setts (e.g., Figure 2). This estimate  
323 compares remarkably well to the total surface area calculated using the area regression  
324 model (eq. 1) (11,454 m<sup>2</sup> or 27 m<sup>2</sup> ha<sup>-1</sup>). These values represent minimum estimates as of  
325 2004, excluding addition smaller diggings.

326

327 Using these surface area data in the volume model (eq. 2), the estimated total volume of  
328 soil excavated during construction of named setts at Wytham is 304.4 m<sup>3</sup> (Table 4). This  
329 excludes five setts for which modelled volumes were slightly negative due to initially small  
330 values of *A*. This estimate is equivalent to about 274 t based on a minimum indicative soil  
331 bulk density of 0.9 Mg m<sup>-3</sup> (Butt et al., 2009). This represents soil displacement rates of  
332 between 0.1 and 1.5 m<sup>3</sup> yr<sup>-1</sup> at individual setts, or a total of between 6.7 and 9.8 m<sup>3</sup> yr<sup>-1</sup>  
333 (6.0–8.8 t) for all setts, depending on whether those of unknown age (already present in  
334 the first survey of the site in 1972 as reported by Kruuk, 1978a) are included in the  
335 calculations (Table 4). The average estimated excavation volume for an individual sett (*E*)  
336 is 4.7 m<sup>3</sup> (about 4.2 t of soil), but ranges from just 0.2 m<sup>3</sup> up to a maximum of 27.8 m<sup>3</sup> (25 t  
337 of soil) for the largest sett ('Great Oak', Table 2).

338

339 *Excavated soil volume 2: extrapolation from individual digging rates*

340 Reconstructions of Mac Bracken (MB) and Pasticks Outlier (PO) sett complexes are  
341 shown in Figure 5a–b. Cut-fill analyses gave total estimated soil excavation volumes of  
342 26.0 m<sup>3</sup> (23.4 t) and 19.3 m<sup>3</sup> (17.4 t) for these two setts, respectively. This is equivalent to  
343 an excavation rate of 2.2 m<sup>3</sup> yr<sup>-1</sup> at MB and 1.9 m<sup>3</sup> yr<sup>-1</sup> at PO.

344

345 Notably, the excavation volumes for MB and PO derived from the 3D reconstructions are  
346 much greater than those calculated using the regression models—by a factor of more than  
347 3 (Table 5). This may be attributed to over-estimation by the reconstruction technique as  
348 this approach assumes the whole sett complex is composed only of soil; in reality, larger  
349 badger sett complexes may include bedding material (grass, leaves, etc. used to line  
350 chambers) that is incorporated into spoil during periods of sett maintenance (Neal &  
351 Cheeseman, 1996, Figure 3d). Even slight inaccuracies in the underlying slope plane may  
352 also influence cut-fill estimates; sensitivity tests using artificially lowered edge point data  
353 indicated that survey inaccuracies in the order of 2 cm yield errors in volume estimates of  
354 about 12%. Excavation volumes calculated using the area and volume regression models  
355 (eq. 1 and eq. 2) are therefore probably better as conservative minimum estimates.

356

357 Nevertheless, 3D reconstruction provides a unique means of estimating individual digging  
358 rates ( $e$ ) that can be extrapolated up to the whole population—something that has proved  
359 extremely difficult in zoogeomorphological studies. Thus, between 1993 and 2004, 10  
360 different badgers contributed 17 excavation years ( $X_{yr}$ , eq. 5) to the construction of MB  
361 sett. Based on a volume of 26.0 m<sup>3</sup> derived from the 3D model, the average annual  
362 excavation rate per badger ( $e$ ) at this sett is 1.53 m<sup>3</sup> yr<sup>-1</sup> (eq. 7, Table 4). This compares  
363 with estimates of annual soil excavation by individual pocket gophers (0.5–1.7 m<sup>3</sup>)

364 reported by Cox & Allen (1987). In marked contrast, a significantly higher number of  
365 excavation years at PO (104 years by 41 unique adult badgers since 1995) yields a much  
366 smaller value of  $e$ , just  $0.19 \text{ m}^3 \text{ yr}^{-1}$ , based on a soil volume of  $19.3 \text{ m}^3$  (Table 4). This  
367 lower value compares remarkably well with the average estimate of  $e$  derived using the  
368 surface area/volume regression models ( $0.21 \text{ m}^3 \text{ yr}^{-1}$ ) (Table 4).

369

370 By substituting these two values of  $e$  (0.19 for PO and 1.53 for MB) into eq. 6 for each sett,  
371 the total excavation volume for the 64 main setts is estimated to be between  $601.4 \text{ m}^3$  (541  
372 t) and  $4,842.5 \text{ m}^3$  (4,358 t). These calculations represent very different annual soil  
373 displacement rates of  $13.1\text{--}19.4 \text{ m}^3 \text{ yr}^{-1}$  and  $113.3\text{--}156.2 \text{ m}^3 \text{ yr}^{-1}$ , respectively, depending  
374 on whether setts > 31 years old are included. Such a large difference in estimated digging  
375 rates is likely explained by the ecological functions of these two setts. In particular, the  
376 fecundity of female badgers (see Table 1) from MB is 1.58 (Table 2), which is the second  
377 highest of all setts and significantly higher than the population average of 0.44.

378 Furthermore, the sex ratio of all previous residents at MB sett is heavily skewed towards  
379 females (Table 2). This indicates that Mac Bracken has functioned as a breeding annex to  
380 which females from the social group in this area of the woods ('Marley Main') move  
381 periodically to give birth (Revilla, Palomares, & Fernández, 2001; Roper, 1992a; Roper,  
382 Ostler, Schmid, & Christian, 2001).

383

384 Setts with high fecundity (such as MB) are expected to have more chambers than other  
385 setts—and therefore likely higher excavation rates—as cubs are thought to be raised in  
386 isolation from other members of the social group (Cresswell, Harris, Cheeseman, &  
387 Mallinson, 1992; Kruuk, 1989). Furthermore, the topographies of breeding annexes likely  
388 reflect greater incorporation of bedding material, as bedding collection and maintenance  
389 behaviors are more frequent and intensive at these setts (Kaneko et al., 2010). By

390 functioning as a breeding annex, a few individuals resident at Mac Bracken (MB) sett  
391 appear to have dug significantly more earth than the many more individuals at Pasticks  
392 Outlier (PO), and over a similar period of time (10 and 12 years, respectively). Similarly,  
393 'The Mount' sett is unusually large relative to its number of excavation years and has the  
394 highest fecundity of any sett (Table 2). These observations suggest that the amount of soil  
395 displaced during the construction and maintenance of Eurasian badger setts is heavily  
396 influenced by its particular social function and the reproductive life-history traits of its  
397 residents (e.g., Stewart et al., 1999). This is a factor that may well have bearing on the  
398 geomorphological impacts of other burrowing animals, particularly those living in social  
399 groups.

400

401 With all this in mind, we regard the very high digging rate ( $e$ ) calculated for Mac Bracken  
402 sett as a probable exception. We therefore favor our more conservative volume  
403 estimations based on: (1) the digging rate ( $e$ ) derived from the reconstruction of Pasticks  
404 Outlier sett ( $0.19 \text{ m}^3 \text{ yr}^{-1}$  per badger), and (2) the surface area/volume regression models.  
405 These preferred methods yield an estimated total soil excavation volume for the 64 named  
406 setts in Wytham Woods of  $304.4\text{--}601.4 \text{ m}^3$  (as of 2004), representing a local digging rate  
407 of  $6.7\text{--}19.4 \text{ m}^3$  ( $6.0\text{--}17.5 \text{ t}$ ) per year at sett sites (Table 4). Averaged over the whole  
408 woodland (424 ha) this equates to a sediment production rate of  $1.42\text{--}4.12 \text{ g m}^{-2} \text{ yr}^{-1}$ .  
409 Encouragingly, our conservative estimate lies within the range previously reported for  
410 Eurasian badgers in the Belgian Ardennes ( $0.05\text{--}12.9 \text{ g m}^{-2} \text{ yr}^{-1}$ , Table II in Voslamber and  
411 Veen, 1985).

412

### 413 **Indirect zoogeomorphological impacts of badgers**

414 *Soil surface cover*



415 Soil cover type varied significantly between sett surface patches (ANOVA  $p < 0.000$ , Table  
416 6). Post-hoc comparisons (Tukey tests) showed that sett mound tops and flanks had  
417 significantly more bare soil than inter-mound and control areas, which had significantly  
418 more litter ( $p < 0.05$ , Figure 6). Eldridge & Myers (2001) report similar patterns for mounds  
419 of the European rabbit (*Oryctolagus cuniculus* L.) associated with disturbance by digging  
420 and trampling. Litter was also observed to accumulate in areas of digging nearby setts,  
421 such as shallow foraging digs and latrines (e.g., Figure 3e), but these were not measured  
422 directly in this study. The boundary between mound flanks and inter-mound areas was  
423 typically well-defined (also observed for European rabbit warrens, Eldridge & Myers, 2001)  
424 and reflects the shedding of litter from mounds and its accumulation around the edges of  
425 sett complexes (e.g., Figure 3f).

426

427 Vegetation cover did not vary significantly between sett patches although clumps of  
428 juvenile plants, especially dog's mercury (*Mercurialis perennis*) and common nettle (*Urtica*  
429 *dioica*), were sometimes present on the flanks of spoil mounds (e.g., Figure 3g) whilst  
430 typically absent from litter-covered control areas. In a recent study in Poland (Kurek et al.,  
431 2014) digging by *M. meles* and foxes (*Vulpes vulpes*) was found to cause a shift in plant  
432 community composition and species richness relative to undisturbed areas. This was  
433 associated with changes in soil physical and chemical properties and endozoochorous  
434 seed dispersal. Digging by other mammals such as pocket gophers and rabbits also alters  
435 plant community composition to varying extents depending on the frequency of soil  
436 disturbance and reworking (Eldridge & Myers, 2001; Huntly & Reichman, 1994). A detailed  
437 assessment of the impacts of *M. meles* on plant communities in Wytham Woods is yet to  
438 be undertaken.

439

440 Stoney material (the Coral Rag through which the badgers dig to reach the preferred  
441 sandy soil below) was found exclusively in areas of badger disturbance (mound tops,  
442 flanks, and inter-mound areas) whilst completely absent from control areas (Figure 6). The  
443 relative occurrence of the Rag is partly dependent on whether setts were built on slopes or  
444 flat ground, and local variations in the thickness and depth of the Rag and grit layers  
445 (Macdonald et al., 2004). Stones were typically graded by size on spoil mound slopes, as  
446 larger stones roll further under gravity during excavation and when mobilized by runoff  
447 flows (e.g., Figure 3h). Hansen and Morris (1968) suggest that the presence of rock or  
448 large stones may inhibit burrowing by pocket gophers, but badgers are clearly able to  
449 manage surprisingly large chunks of the Rag (mean dimensions were 10 x 5 x 4 cm and  
450 the largest piece found in spoil was 25 x 18 x 16 cm,  $n = 30$ ).

451

#### 452 *Spoil erodibility*

453 Martin (2003) suggests that bioturbated soils exhibit differences in infiltration and runoff  
454 characteristics as a function of mineral, chemical, and organic composition, and properties  
455 such as water repellency. Such variables affect erosion rates by altering the time required  
456 for the infiltration of raindrops and the generation of surface flows capable of particle  
457 entrainment and transport (e.g., Wessel, 1988). At Wytham, badger spoil had a higher  
458 proportion of sand- (54%) and gravel-sized (16%) material compared to undisturbed soils  
459 (32% and 3%, respectively) (Figure 7), reflecting the displacement of grit sands and Coral  
460 Rag from lower horizons. Unconfined compressive strength also varied significantly  
461 between sett patches and control areas (ANOVA  $p < 0.000$ , Table 7), with freshly-dug  
462 spoil being 58% weaker than control soils ( $p = 0.01$ , Figure 8). Water Drop Penetration  
463 Times (WDPT) were less than one second for badger spoil compared to an average of 220  
464 seconds for control soils ( $n = 20$ ). Fresh spoil is therefore 'very hydrophilic' and  
465 undisturbed soils 'moderately hydrophobic' according to the classifications of Bisdom,

466 Dekker, & Schoute (1993) and Doerr (1998). Similarly, aggregate breakdown was three  
467 orders of magnitude faster for fresh spoil in wet and dry stability tests compared to control  
468 soils (Figure 9).

469

470 Comparison of the relative grain size populations for fresh and crusted badger spoil  
471 (Figure 7) shows that once exposed at the surface, fresh spoil supplies fine sediment (<  
472 200  $\mu\text{m}$  in diameter) for erosion via rainsplash and surface wash (e.g., Borchard &  
473 Eldridge, 2011). Indeed, removal of fines can occur within just a few precipitation events.  
474 Once in transport, material is moved to the periphery of mounds and may become  
475 incorporated into soils or move further downslope depending on the underlying gradient  
476 (Ellison, 1946; Gabet, 2000; Price, 1971; Wilkinson et al., 2009). In this way animal spoil  
477 can be a dominant source of material for erosion in many environments (e.g., Black &  
478 Montgomery, 1991; Butler, 1995; Gabet, 2000; Thorn, 1978; Yair, 1995). As occupied setts  
479 remain free from a protective cover of litter (Figure 6) and have a greater proportion of  
480 mobile fine sediment exposed on their surfaces, digging by Eurasian badgers represents  
481 an important component of the sediment budget in the temperate woodlands they inhabit.  
482 Further direct comparisons of soil transport rates in control and sett areas would provide  
483 interesting data to support these observations.

484

485 In contrast to freshly-dug spoil, there is evidence of rapid stabilization via the removal of  
486 fines, and surface compaction and relaxation (Butler, 1995; Eldridge, 2004; Eldridge &  
487 Myers, 2001; Eldridge & Simpson, 2002). At Wytham, older sett surfaces were stronger  
488 than control soils ( $p = 0.01$ , Figure 8), and while dried aggregates from older mounds  
489 broke down at a similar rate to crusted spoil, they were considerably more stable than  
490 fresh spoil in wet stability tests (Figure 9). Soil aggregates from the base of old mounds  
491 were most stable in dry and wet tests (Figure 9). Hard stony lag deposits were typical for

492 older spoil (Figure 3h, Figure 6), which may be further hardened by cementation of muds  
493 and clays following rainfall (Figure 8). Shedding of litter and stones from older mound  
494 slopes is probably associated with the higher rates and deeper runoff flows that they  
495 appear to generate. Of all sett patches, badger paths were most stable ( $p = 0.01$ , Figure  
496 8), attributed to compaction by generations of badgers during nightly foraging trips (Kruuk,  
497 1978b, 1989). These paths may well represent preferential routes for surface water flows.  
498  
499 These observations indicate that badger sett bioconstructions represent landforms of  
500 overall relative stability, but from which supply of fine material for subaerial processes  
501 periodically occurs—at a rate determined by the frequency of badger disturbance. The fact  
502 that badgers do not occupy all parts of their setts at any one time—around 80% of 1,130  
503 entrance holes were actively being used in Wytham Woods in 2002 (Macdonald et al.,  
504 2004)—means that sett complexes consist of both relatively stable, older spoil deposits  
505 and more recently dug, highly-erodible deposits.

506

## 507 **5. Conclusions**

508 Three decades of ecological data for a population of Eurasian badgers in Wytham Woods  
509 have been used to assess local- and landscape-scale zoogeomorphic impacts in terms of  
510 direct (sett excavation) and indirect (spoil erodibility) contributions to sediment  
511 displacement, storage, and transport. Whilst our extrapolations assume equal individual  
512 digging effort, we have, for the first time, been able to account for unevenness in  
513 geomorphic impact arising from differences in individual sett fidelity. Further work is now  
514 needed to develop and test these zoogeomorphological models in order to account for  
515 more of the ecological complexity associated with animal populations.

516

517 We estimate that individual badgers in Wytham Woods dig between 0.19–4.51 m<sup>3</sup> of soil  
518 per year depending on the sett they are associated with, the ecological function of that  
519 sett, and the life-history traits of the individual. Taking values derived from the regression  
520 models and reconstruction of Pasticks Outlier as being most representative, a minimum  
521 total of 274–541 t of earth has been displaced during the construction of 64 setts (based  
522 on 2004 data). This equates to a spatially-averaged sediment production rate of 1.42–4.12  
523 g m<sup>-2</sup> yr<sup>-1</sup> (6.0–17.5 t per year in sett areas). Locally, badger setts themselves represent  
524 unique landforms in European woodland habitats that appear to have been largely  
525 overlooked in a geomorphological context compared to those of burrowing animals in other  
526 environments (e.g., Gabet et al., 2014). The construction of badger setts—the  
527 characteristics of which are largely driven by ecological factors—involves the direct and  
528 often rapid displacement of significant amounts of soil.

529

530 Once excavated, the indirect geomorphological significance of setts (with respect to  
531 sediment erosion and transport) depends on the relative proportion of new (freshly dug)  
532 and older (stabilized) surfaces. Importantly, material brought to the surface by badgers  
533 during the continual reworking, maintenance, and extension of setts creates patchy soil  
534 conditions on which subaerial processes act at varying rates (e.g., Gabet et al., 2003).  
535 Similar to other parts of Europe (e.g., Kurek et al., 2014), fresh badger spoil in Wytham  
536 Woods had a higher proportion of sand, and our measurements show that this material  
537 has lower structural stability than undisturbed soils and is susceptible to erosion by water.  
538 Spoil mounds are quickly stabilized following the removal of fines (over a few rainfall  
539 events) and the gradual development of cemented and compacted lag deposits. Well-  
540 established badger setts are therefore relatively stable bioconstructions that persist in the  
541 landscape for decades and probably centuries, but which periodically contribute highly-  
542 erodible material to local sediment budgets.

543

544 As well as presenting some of the first assessments of population-level zoogeomorphic  
545 impacts, this study highlights the importance of both biotic and abiotic factors in  
546 constraining the spatial and temporal patterns of digging by burrowing animals (e.g., Gabet  
547 et al., 2014; Johnson et al., 2002; Macdonald, Mitchelmore, & Bacon, 1996; Macdonald et  
548 al., 2004; Obidziński, Pabjanek, & Mędrzycki, 2013; Revilla et al., 2001). The availability of  
549 suitable substrate, local topography, and density dependent interactions between social  
550 groups are particularly important for Eurasian badgers. Such factors need to be identified  
551 and quantified more fully in future zoogeomorphological investigations if generalized, rule-  
552 based models capable of evaluating landscape-scale impacts are to be developed and  
553 constrained (e.g., Gabet et al., 2014; Schiffers, Teal, Travis, & Solan, 2011). Data  
554 generated from spoil measurements (volumes, mounding rates, decay rates, frequency of  
555 reworking, etc.) are clearly critical to future work, but effort should also be made to collect  
556 and utilize long-term ecological (i.e., population) and environmental data where available.

557

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563

564

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Sett Variable	Description
<i>Sett age</i>	Minimum number of years a sett has existed (31 years is the minimum age for setts identified in Kruuk 1978a; 18 years for setts present at the first capture (1987); absolute age of setts < 18 years is known from trapping records).
<i>Independence age</i>	Minimum number of years since a sett has been socially independent from other setts, having its own established territory.
<i>Unique residency</i>	Total minimum number of unique adult badgers ever trapped at a sett since 1987.
<i>Males</i>	Minimum total number of unique adult males ever trapped at a sett since 1987.
<i>Females</i>	Minimum total number of unique adult females ever trapped at a sett since 1987.
<i>Sex ratio</i>	Proportion of adult females to adult males comprising total unique residency.
<i>Sett fecundity</i>	Total number of unique cubs ever trapped at a sett.
<i>Female fecundity</i>	Mean number of cubs per unique female resident of a sett.
<i>Excavation years (<math>X_{yr}</math>)</i>	Cumulative total years' residency of all unique badgers.
<i>Fidelity</i>	Mean number of years each unique adult remained resident at a sett.

**Table 1.** Sett variables determined for every member of the badger population recorded in the Wytham Trapping Database as of 2004 (raw data supplied by WildCRU, Department of Zoology, University of Oxford).

Sett ID	Minimum age (yrs)	Surface area <sup>a</sup> (m <sup>2</sup> )	Entrance holes	Unique residency	Excavation years ( $X_{yr}$ )	Sex ratio (f:m)	Fidelity (yrs)	Sett fecundity	Female fecundity	Excavation volume <sup>b</sup> (m <sup>3</sup> )
BB	31	300*	10	54	98	1.33	1.81	21	0.50	8.9
BP	18	80	5	38	98	0.96	2.58	10	0.20	2.3
CH	31	147	12	80	189	1.25	2.36	33	0.39	4.3
CLO	7	55	3	21	39	0.56	1.86	6	0.24	1.5
FB	10	225	9	28	69	0.77	2.46	17	0.44	6.6
GATES	6	32	9	13	22	1.20	1.69	6	0.60	0.8
GO	31	930	26	62	142	0.46	2.29	52	0.54	27.8
GOA	6	20	2	6	7	0.40	1.17	1	0.20	0.5
GW	18	218	5	42	82	1.05	1.95	10	0.25	6.4
HC	18	128	11	50	117	1.13	2.34	24	0.44	3.7
HCFO	11	24	4	17	23	0.64	1.35	8	0.57	0.6
HCMO	8	12	3	6	6	5.00	1.00	1	1.00	0.2
HCT	2	37	2	5	5	0.67	1.00	0	0.00	1.0
HH	18	136*	9	36	71	1.22	1.97	8	0.25	3.9
JH	18	189	10	39	121	1.47	3.10	18	0.37	5.5
JkBr	8	400*	8	5	7	0.75	1.40	4	1.00	11.9
KH	10	144	10	28	52	0.73	1.86	5	0.17	4.2
M2	17	86	5	22	41	0.95	1.86	18	0.86	2.4
McBr	12	248	10	10	17	0.42	1.70	19	1.58	7.3
MT	31	744	29	19	30	0.88	1.58	26	1.63	22.2
O1	18	35	4	38	59	1.27	1.55	10	0.38	0.9
P	18	546	10	67	197	0.70	2.94	41	0.35	16.2
PO	10	200	4	41	104	1.08	2.54	17	0.34	5.9
RC	18	260	22	47	121	1.15	2.57	18	0.31	7.7
RCO	10	48	7	32	32	0.45	1.00	5	0.23	1.3
SH	18	300	n.d.	60	167	1.09	2.78	25	0.31	8.9
TC	31	150*	10	48	102	0.55	2.13	38	0.58	4.4
TCB	5	40*	4	15	23	0.44	1.53	1	0.06	1.1
UF	17	100	5	22	28	0.75	1.27	22	1.38	2.9

<sup>a</sup>minimum surface area of disturbed soil (\* indicates partially-obstructed setts for which surface area was visually estimated)

<sup>b</sup>volume estimated from surface area data using regression modelling (eq. 2)

**Table 2.** Sett variables determined for visited setts ( $n = 29$ , data for the other 35 named setts are not shown here). Surface area and number of entrance hole were determined in the field (in 2005); excavation volumes were estimated using regression modelling (see text); all other parameters are derived from the Wytham Trapping Database (see Table 1). Surveyed and reconstructed setts (Mac Bracken and Pasticks Outlier) are shaded. n.d. indicates no available data.

Bioconstruction	Location of study	Surface area (m <sup>2</sup> )	Height (m)	Reference
Eurasian badger setts ( <i>Meles meles</i> )	Central southern England	12–930	0.2–2.0	This study
	Belgium	14.7 <sup>a</sup>	n.d.	Voslamber & Veen, 1985
European rabbit warrens ( <i>Oryctolagus cuniculus</i> )	Southern Australia	200 <sup>b</sup>	0.1–0.2	Eldridge & Myers, 2001
Wombat warrens ( <i>Lasiorhinus latifrons</i> )	Southern Australia	314–707 <sup>c</sup>	0.5–1.0	Löffler & Margules, 1980
Arctic fox dens ( <i>Alopex lagopus</i> )	Northwestern Canada	123–130	2.1–4.5	Smits, Smith & Slough, 1988
Giant Kangaroo Rat mounds ( <i>Dipodomys ingens</i> )	Western USA	38–79 <sup>d</sup>	0.5–2.0 <sup>e</sup>	Prugh & Brashares, 2012
Prairie dog mounds ( <i>Cynomys ludovicianus</i> )	Central America	4.9 <sup>f</sup>	1	Cincotta, 1989
Mima mounds (assuming pocket gopher origin, Geomyidae)	Northwestern USA	0.8–707 <sup>g</sup>	0.1–2.0	Johnson & Horwath Burnham, 2012

<sup>a</sup>assuming a circular sett planform of 4.32 m mean diameter

<sup>b</sup>text description

<sup>c</sup>assuming a circular mound planform of 20–30 m diameter

<sup>d</sup>assuming a circular mound planform of 7–10 m diameter

<sup>e</sup>based on visual inspection of Plate 1 in Prugh & Brashares, 2012

<sup>f</sup>assuming a circular mound planform of 2.5 m diameter

<sup>g</sup>assuming a circular mound planform of 1–30 m diameter

**Table 3.** Some indicative dimensions of burrowing animal bioconstructions (n.d. indicates no data).

Calculation method	Per badger excavation rate (e), m <sup>3</sup> yr <sup>-1</sup>	Total excavation volume for Wytham Woods, m <sup>3a</sup>	Local excavation in rate (in sett areas), m <sup>3</sup> yr <sup>-1b</sup>	Spatially-averaged sediment production, g m <sup>-2</sup> yr <sup>-1c</sup>
Regression modelling	0.21 <sup>d</sup>	304.4	6.7–9.8	1.4–2.1
Extrapolation from Pasticks Outlier (PO) sett 'e'	0.19	601.4	13.1–19.4	2.8–4.1
Extrapolation from Mac Bracken (MB) sett 'e'	1.53	4,842.5	113.3–156.2	24.1–33.2

<sup>a</sup>for 64 named setts, as of 2004

<sup>b</sup>annual excavation rate over a minimum total sett surface area of 1.15 ha; lower and upper estimates exclude and include setts of unknown age (> 31 years), respectively, based on Kruuk 1978a

<sup>c</sup>spatially-averaged rate based on a total area for Wytham Woods of 424 ha

<sup>d</sup>mean value of 'e' for all setts, derived from regression model estimates of volume in each case

**Table 4.** Badger mound excavation volumes and rates estimated from two different methods: (1) regression modelling using surface area, and (2) extrapolation from individual badger digging rates, e, determined for two different setts.

	Estimated Volume of Soil (m <sup>3</sup> )	
	Regression modelling	3D modelling
Mac Bracken sett (MB)	7.3	26.0
Pasticks Outlier sett (PO)	5.9	19.3

**Table 5.** Comparison of sett excavation volumes derived for two setts using: (1) regression models based on surface area and ecological sett data, and (2) GIS reconstructions from field survey data and cut-fill analysis.

<b>Source</b>	<b>d.f.</b>	<b>MS</b>	<b>F</b>	<b>P</b>
Sett patch ( $n = 3$ )	3	35.52	0.00	0.999
Cover type ( $n = 4$ )	8	13799.77	49.08	< 0.000
Residuals	228	281.16	–	–
Total	239	–	–	–

Cochran's test for heterogeneity = 0.159, not significant

**Table 6.** Analysis of variance for surface cover (bare soil, litter, and vegetation) nested in sett surface patch (spoil mound top, spoil mound flank, inter-mound area, control),  $n = 20$  per patch, see Figure 6.

<b>Source</b>	<b>d.f.</b>	<b>MS</b>	<b>F</b>	<b>P</b>
Sett patch ( $n = 4$ )	3	5.401	124.34	< 0.000
Residuals	116	0.0434	—	—
Total	119	—	—	—

Data square-root transformed; Cochran's test for heterogeneity = 0.386, not significant

**Table 7.** Analysis of variance for soil penetration strength between sett surface patches (fresh spoil, older spoil, badger path, control),  $n = 30$  per patch, see Figure 8.

## Figure captions

**Figure 1.** A typical spoil mound of the Eurasian Badger (*Meles meles*). Multiple mounds coalesce to form larger sett surface complexes.

**Figure 2.** The distribution of named badger setts at Wytham Woods, Oxfordshire (2004 data supplied by WildCRU, Department of Zoology, University of Oxford). Location of Calcareous Grit Sand layer in which the majority of setts are dug is also shown, digitized from Kruuk 1978a. Reconstructed setts (Mac Bracken and Pasticks Outlier) are indicated.

**Figure 3.** Features of badger bioturbation in Wytham Woods: (a) characteristic sandy spoil, (b) spoil with stony Coral Rag incorporated, (c) topographic depression resulting from burrow entrance collapse, (d) bedding material recently cleared from a burrow entrance, (e) litter accumulation in a badger dig, (f) well-defined mound/inter-mound boundary illustrating shedding of material from compact mound slopes, (g) vegetation growing on a badger mound, (h) size-sorting of stones on a sett slope.

**Figure 4.** Minimum population size of badgers (solid line) and number of newly constructed setts (dashed line) between 1987 and 2004. A statistically significant correlation exists factoring in a 3-year lag ( $R^2 = 0.67$ ,  $p = 0.006$ ).

**Figure 5.** Three-dimensional models of: (a) Mac Bracken Sett (MB) and; (b) Pasticks Outlier sett (PO) reconstructed from field-survey data using GIS. Pre-disturbance (top), sett complex (middle) and cut-fill (bottom) surfaces shown. Planform maps (0.1m interpolated contours) and pre- and post-disturbance cross-section profiles also shown (color versions available online).

**Figure 6.** Mean (+ SD,  $n = 20$ ) surface cover (%) of bare soil, litter, vegetation, and stones for different sett surface patches and control areas.

**Figure 7.** Relative proportions of mud, sand, and gravel (%) for soil samples (< 5 cm depth,  $n = 5$ ) for different sett surface patches and control areas.



**Figure 8.** Mean soil penetration strength (+ SD,  $n = 30$ ) in different sett patches and control soils.

**Figure 9.** Wet and dry aggregate stability for samples taken from different sett surface patches and control areas (\*breakdown time for dry fresh spoil was instantaneous).