

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

3
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7
8 **ABSTRACT**

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

14 Using a unique ecological dataset for Eurasian badgers (*Meles meles* L.) in Wytham
15 Woods, Oxfordshire, UK, we show that direct zoogeomorphological impact (soil
16 displacement during sett excavation) is constrained by fluctuations in overall population
17 size. Modelled digging rates for individual badgers (0.19–4.51 m³ yr⁻¹) varied depending on
18 the ecological function of the sett they are associated with, and we estimate that the whole
19 population has displaced 304–601 ± 72 m³ of soil during the construction of 64 setts. This
20 represents an overall excavation rate of 6.7–19.4 m³ (6.0–17.5 t) yr⁻¹ in sett areas, or 1.42–
21 4.12 g m⁻² yr⁻¹ when averaged over the whole 424 ha woodland.

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

26
27 **KEY WORDS:** Burrowing, biogeomorphology, bioturbation, *Meles meles*, ecosystem
28 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, Jermlmack, 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 m³ 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

106 construct burrows, badgers may dig shallow foraging pits (or 'scrapes', Wilkinson et al.,
107 2009) when searching for earthworms and other foodstuffs (Kruuk, 1978b).

108

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

121

122 **Study site**

123 Wytham Woods (OS SP 462 080) occupy 424 ha of land 5 km north-west of the City of
124 Oxford, UK (Figure 2). The woods lie over two outlying hills of the Cotswold Escarpment
125 (Wytham Hill and Seacourt Hill) varying in altitude from 60–165 m above sea level
126 (Macdonald, Newman, Dean, Buesching, & Johnson, 2004). Geology consists of Middle
127 Jurassic Coral Rag topped with clayey soils from the Sherbourne and Morton series that
128 rest on Lower Calcareous Grit sands. This characteristically orange-yellow sand encircles
129 the two hills (Figure 2) and is the preferred digging medium for the badgers (Hofer, 1988;
130 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 km²). Setts had a density of about 70 per km², 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
$$A = 8.7a + 1.0X_{yr} + 15.5c - 7.2u - 20.7$$
 (eq. 1)

168 where A = sett surface area (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
$$V = 0.03A - 0.14$$
 (eq. 2)

178 where V = sett subsurface volume (m^3) and A = minimum sett surface area (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 m² 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 m²) 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 (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 m². 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 m²). This is equivalent to just 28 m² ha⁻¹ 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 m² or 27 m² ha⁻¹). 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 m³ (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⁻³ (Butt et al., 2009). This represents soil displacement rates of
332 between 0.1 and 1.5 m³ yr⁻¹ at individual setts, or a total of between 6.7 and 9.8 m³ yr⁻¹
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 m³ (about 4.2 t of soil), but ranges from just 0.2 m³ up to a maximum of 27.8 m³ (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 m³ (23.4 t) and 19.3 m³ (17.4 t) for these two setts, respectively. This is equivalent to
343 an excavation rate of 2.2 m³ yr⁻¹ at MB and 1.9 m³ yr⁻¹ 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 m³ derived from the 3D model, the average annual
362 excavation rate per badger (e) at this sett is 1.53 m³ yr⁻¹ (eq. 7, Table 4). This compares
363 with estimates of annual soil excavation by individual pocket gophers (0.5–1.7 m³)

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 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 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 μm 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 m³ 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⁻² yr⁻¹ (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

558 **Acknowledgements**

559 Dr. Christopher Newman, and members of WildCRU and the Wytham Badger Project
560 (Department of Zoology, University of Oxford) are thanked for permissions to access
561 Wytham Woods and for providing data from the Wytham Trapping Database. Dr. Parris
562 Lyew-Ayee (University of the West Indies) is thanked for invaluable GIS assistance.

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 (X_{yr})</i>	Cumulative total years' residency of all unique badgers.
<i>Fidelity</i>	Mean number of years each unique adult remained resident at a sett.

815

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

819

820

Sett ID	Minimum age (yrs)	Surface area ^a (m ³)	Entrance holes	Unique residency	Excavation years (X _{yr})	Sex ratio (f:m)	Fidelity (yrs)	Sett fecundity	Female fecundity	Excavation volume ^b (m ³)
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

847

848 ^aminimum surface area of disturbed soil (* indicates partially-obstructed setts for which surface area was visually estimated)849 ^bvolume estimated from surface area data using regression modelling (eq. 2)

850

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

Bioconstruction	Location of study	Surface area (m ²)	Height (m)	Reference
Eurasian badger setts (<i>Meles meles</i>)	Central southern England	12–930	0.2–2.0	This study
	Belgium	14.7 ^a	n.d.	Voslamber & Veen, 1985
European rabbit warrens (<i>Oryctolagus cuniculus</i>)	Southern Australia	200 ^b	0.1–0.2	Eldridge & Myers, 2001
Wombat warrens (<i>Lasiorhinus latifrons</i>)	Southern Australia	314–707 ^c	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 ^d	0.5–2.0 ^e	Prugh & Brashares, 2012
Prairie dog mounds (<i>Cynomys ludovicianus</i>)	Central America	4.9 ^f	1	Cincotta, 1989
Mima mounds (assuming pocket gopher origin, Geomyidae)	Northwestern USA	0.8–707 ^g	0.1–2.0	Johnson & Horwath Burnham, 2012

855 ^aassuming a circular sett planform of 4.32 m mean diameter

856 ^btext description

857 ^cassuming a circular mound planform of 20–30 m diameter

858 ^dassuming a circular mound planform of 7–10 m diameter

859 ^ebased on visual inspection of Plate 1 in Prugh & Brashares, 2012

860 ^fassuming a circular mound planform of 2.5 m diameter

861 ^gassuming a circular mound planform of 1–30 m diameter

862

863

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

866

867

Calculation method	Per badger excavation rate (e), m ³ yr ⁻¹	Total excavation volume for Wytham Woods, m ^{3a}	Local excavation in rate (in sett areas), m ³ yr ^{-1b}	Spatially-averaged sediment production, g m ⁻² yr ^{-1c}
Regression modelling	0.21 ^d	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

868 ^afor 64 named setts, as of 2004

869 ^bannual excavation rate over a minimum total sett surface area of 1.15 ha; lower and upper estimates
870 exclude and include setts of unknown age (> 31 years), respectively, based on Kruuk 1978a

871 ^cspatially-averaged rate based on a total area for Wytham Woods of 424 ha

872 ^dmean value of 'e' for all setts, derived from regression model estimates of volume in each case

873

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

877

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

878
879 **Table 5.** Comparison of sett excavation volumes derived for two setts using: (1) regression
880 models based on surface area and ecological sett data, and (2) GIS reconstructions from
881 field survey data and cut-fill analysis.

882
883

884

Source	d.f.	MS	F	P
Sett patch ($n = 3$)	3	35.52	0.00	0.999
Cover type ($n = 4$)	8	13799.77	49.08	< 0.000
	22			
Residuals	8	281.16	–	–
	23			
Total	9	–	–	–

885 Cochran's test for heterogeneity = 0.159, not significant

886

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

890

891

892

Source	d.f.	MS	F	P
Sett patch ($n = 4$)	3	5.401	124.34	< 0.000
	11			
Residuals	6	0.0434	–	–
	11			
Total	9	–	–	–

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

894

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

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900 **Figure captions**

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

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

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

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

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

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

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

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

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

929