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Anticipation of common buzzard population patterns in the changing UK landscape

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Yes

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The following data files are available for public use through the Dryad Digital Repository via the following link: <http://dx.doi.org/10.5061/dryad.8n183>. ALBAUT (with any extension, location data from 114 radio-tagged buzzards). Land Cover Map of Great Britain is available against permission at public site, <http://www.ceh.ac.uk/services/land-cover-map-1990>.

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1 **Anticipation of common buzzard population patterns in the changing UK**
2 **landscape**

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19 Abstract

20 Harmonious coexistence between humans, other animals and ecosystem services they support is a
21 complex issue, typically impacted by landscape change which affects animal distribution and
22 abundance. In the last 30 years, afforestation on grasslands across Great Britain has been increasing,
23 motivated by socio-economic reasons and climate change mitigation. Beyond expected benefits, an
24 obvious question is what are the consequences for wider biodiversity of this scale of landscape
25 change. Here we explore the impact of such change on the expanding population of common
26 buzzards *Buteo buteo*, a raptor with a history of human-induced setbacks. Using Resource-Area-
27 Dependence Analysis, with which we estimated individual's resource needs using 10-day radio-
28 tracking sessions and the 1990's Land Cover Map of GB, and Agent-Based Modelling, we predict
29 that buzzards in our study area in lowland UK had fully recovered (to 2.2 ind/km²) by 1995. We
30 also anticipate that the conversion of 30%, 60% and 90% of economically-viable meadow into
31 woodland would reduce buzzard abundance non-linearly by 15%, 38% and 74%, respectively. The
32 same approach used here could allow for cost-effective anticipation of other animals' population
33 patterns in changing landscapes, thus helping harmonise economy, landscape change and
34 biodiversity.

35

36 **Keywords:** future landscape | ecosystem management | complex system | individual-based
37 modelling | home-range | remote sensing

38 **Introduction**

39 Worldwide, damaging imbalances in animal populations have been driven by anthropogenic
40 landscape alterations that are now being further destabilised by climate change [1]. The impacts of
41 such imbalances on ecosystem services and human livelihoods have already been severe, and will
42 likely get more so. Examples span increases in crop pests, reductions in pollinators and extinctions
43 of iconic species [1]. Hopes of remediation depend on advances in understanding of restoration of
44 wildlife, landscapes and their services [1,2]. Considering the connectedness of ecological processes,
45 there are opportunities for powerful synergies. For example, reintroduction of a predator to mediate
46 herbivore impacts on plants, or creation of urban green mosaics with culturally important animals in
47 mind, can promote a cascade of desirable outcomes including climate change adaptation and
48 mitigation, food production, water security, economic prosperity and human mental health [1,3,4].
49 Even a landscape modification as simple as planting trees in an agricultural area for predatory birds
50 to roost can lead to pest control and thereby increase yield [5–7].

51
52 One example of land use change that is both important in itself and an insightful model from which
53 wider lessons can be drawn is the increase by 5236 km², over the 25 years from 1990 to 2015, of
54 woodland in the UK. This increase has come largely at the expense of grassland [8], motivated by
55 woodland's role in flood management, timber's value for construction, and vegetarianism/veganism
56 reducing the need for grassland to feed livestock [9–11]. Recently, this afforestation process gained
57 further momentum due to the imperative to mitigate climate change and associated pledges to plant
58 millions of trees in the UK for carbon sequestration [12]. However, beyond expected socio-
59 economic and climate benefits, an obvious question is what are the consequences for wider
60 biodiversity of this scale of change in the UK landscape [13,14]. Good practice requires that
61 societies should consider the holistic cascade of effects of their interventions.

62

63 The common buzzard *Buteo buteo* is a medium-sized generalist raptor that in the UK has suffered
64 periodic declines due to human intervention. Over 500 years ago they were regarded as vermin and
65 payments were made for their corpses. Then gamebird rearing and shooting at the end of the 18th
66 century eradicated buzzards from much of eastern Britain. This decline was further exacerbated in
67 the 1950's by the depletion of a key resource, rabbits *Oryctolagus cuniculus*, infected with the
68 myxomatosis virus [15] - the last impact was an unintended outcome of human meddling which had
69 ill-considered epizootiological consequences. Nowadays, general attitudes towards buzzards in the
70 UK are more positive, with only occasional, local episodes of human-wildlife conflict attributed to
71 'problem individuals', which prey on poultry or game birds [16]. The buzzard's resource
72 requirements in lowland UK are clear cut: a tree for nesting and roosting, open areas of grassland,
73 especially 'seasonally-long-grass' (meadow), and rough-ground (combination of sparse grass, open
74 shrub and dense shrub areas) for hunting [17]. The expansion of woodland underway in the UK is,
75 thus, impacting buzzards in at least two opposing ways: an increase in potential roosting sites
76 (trees), but a decrease in foraging sites (meadows). Our objective was to investigate how this
77 change in key resources will play out for buzzards.

78

79 We built an Agent-Based Model (ABM) in which virtual buzzards populated a land-cover map of
80 the 1990's lowland UK. In this landscape, we also explored the consequences for the buzzard
81 population of the gradual replacement of meadow fields of economically-viable size (≥ 20 ha) by
82 woodland for timber extraction and climate change mitigation [11,18]. Model predictions were
83 assessed by comparison with knowledge of wild buzzards according to five dimensions of their
84 spatial ecology, namely home-range area, perimeter, pairwise overlaps and population distribution
85 and abundance. Since two home-ranges can have the same areas and yet different perimeters, and
86 vice-versa, home-range area and perimeter are two proxies for energy expenditure from movement
87 to acquire resources which could differ according to buzzard foraging behaviour. Pairwise home-
88 range overlaps are a proxy for territorial spacing. Our first results are predictions for buzzard

89 maximum distribution and abundance in our focal study area in the 1990's and in plausibly
90 afforested future UK landscapes. In addition, we predict the geographic arrangements of buzzard
91 territories and home ranges. These individual-level insights have practical implications for, for
92 example, the management of 'problem buzzards' via translocations. This opens the door to the
93 general power of the novelty of our approach, which was the creation of an ABM in which the
94 resource parameters were estimated from wild buzzards using Resource-Area-Dependence Analysis
95 (RADA). With RADA, we translated the Land Cover Map of Great Britain (LCMGB) of 1990 [19]
96 into a map of buzzard key resources, estimated the minimum area of each key resource-containing
97 category that the average individual buzzard needs, and discovered within which vicinity of the
98 roosting site each food resource is typically found. The RADA process has conceptual parallels to
99 the Resource Dispersion Hypothesis, which postulates that territory size depends on the dispersion
100 of the resources needed for survival and reproduction, and which has been used to explain the
101 territories of >40 species in five continents [20]. Using the model presented here, predictions
102 considering larger extents of lowland UK, or other realistic landscape change scenarios, could be
103 explored to understand the impact of landscape change on individual buzzards and their
104 populations. We think this same approach could be used efficiently to anticipate the consequences
105 of landscape change on many other animals, thus aiding practical decision making for biodiversity
106 conservation and landscape management.

107

108 **Materials and methods**

109 **Brief characterisation of buzzard space use**

110 Individual buzzard home-ranges, resource use and reproduction were quantified in Dorset, southern
111 UK. Between 1990 and 1995, 114 home-ranges were recorded from 72 radio-tagged buzzards.
112 Nests were counted and transect (T) and Mark-Resighting (M-R) buzzard counts were conducted
113 [15]. Each radio-tracked animal in this sample was wild, had not been previously trapped or

114 relocated, and was not preferably trapped over others on the basis of any characteristic other than
115 our ability to reach the nest—they were therefore not STRANGE animals [21]. Home-ranges were
116 estimated from standardized sets of 30 locations collected for each animal, by recording coordinates
117 three times daily during a 10-day period that was either continuous or separated by a weekend.
118 Estimations based on polygons, kernels and nearest neighbour (cluster) algorithms were tested. It
119 was observed, for example, that home-ranges tend to be mononuclear [22]. Cores including more
120 than 85% of locations seem to include excursions in flight not related to foraging, such as for social
121 reasons [15]. In the study area, juveniles constituted about 10% of the population, and about 90% of
122 them dispersed from the parental territory within 1 year of fledging, indicating their role in the
123 partitioning of space and use of resources was minor when compared to adults [23]. After dispersal,
124 buzzards try to establish their own territory, preferably in a previously unoccupied area [24]. If one
125 is established, usually within the first two years of life, they will typically defend it throughout their
126 lives [15]. No sex-based differences in resource use were found during the pre-breeding season
127 [25]. The landscape at the time of tracking was a translation of the LCMGB of 1990 into a map
128 depicting only the key resource-containing map categories for buzzards (figure S2). This translation
129 was for the resources identified by RADA [17].

130

131 **Modelling**

132 We followed a Pattern Oriented Modelling approach (POM) [26]. The model description follows
133 the ODD (Overview, Design concepts, and Details) protocol [27] and the model itself was created
134 in NetLogo v6.0 [28] and analysed in R [29]. RADA was applied using Ranges 9 [30]. The
135 Supplementary Information is a TRACE document [31].

136

137 ***1. Purpose***

Our primary purpose was to predict the distribution and abundance of common buzzards in the geographical space of the real landscape in lowland UK i) in the 1990's and ii) in landscape change scenarios depicting a gradual replacement of meadow for woodland, motivated by socio-economic reasons and climate change mitigation. Our secondary purpose was to predict buzzard home-ranges and territories.

143

2. Entities, state variables and scales

Entities and state variables are presented in table 1.

146

Table 1

148

The study area was 22 km x 6 km (128k m² of land-cover and 4 km² of seawater) with grain size of 25 m x 25 m (the pixel size of LCMGB of 1990). Most of the land-covers occurring in lowland UK were present in the study area [25]. To avoid edge effects, a boundary strip of length equivalent to the mean largest span of wild buzzard home ranges was included around the study area; virtual buzzards with settling-sites outside the study area could defend patches within it but were not considered in the abundance or distribution predictions, on the assumption that their incursive areas were balanced by excursive areas of those settled within the study area. Temporal scale was not explicitly represented because the focus was in discovering the maximum values for distribution and abundance of a saturated population, no matter how long it took for the buzzards to reach that density.

159

160 3. Process overview and scheduling

161 The model's high-level algorithm is presented in figure 1.

162

163 Figure 1

164

165 1. The run starts with the unpopulated buzzard resource map, which is based on a translation of the
166 LCMGB of 1990 using RADA.

167

168 2. A virtual buzzard settles on an undefended woodland patch, which becomes its roosting site. It
169 will defend this patch (*my-roost* in Table 1) and use it as the base from which to search for its key
170 resources and establish a territory.

171

172 3. The virtual buzzard will then randomly choose a free rough-ground pixel within its rough-ground
173 foraging distance (*rgr-dist*). In finding one, it will fly to it. This will be the seed from where it will
174 search the entire landscape patch.

175

176 4. From the seed, the virtual buzzard begins an iterative search for its free neighbouring pixels of
177 rough-ground, incorporating each into the territory (as *my-rgr*).

178

179 5. Then, when no free rough-ground neighbouring pixels are left, the virtual buzzard will search for
180 rough-ground pixels at the edges of the raster landscape patch it is incorporating into its territory
181 and check whether these have free rough-ground neighbours. If any of them has, the virtual buzzard
182 will iteratively move to each edge pixel with a free rough-ground neighbour, set it as a new base
183 and apply the iterative neighbour search described in 4. When the landscape patch under scrutiny
184 has been fully incorporated into the territory, the virtual buzzard will move back to its roosting site
185 and continue the search for additional free rough-ground patches (by repeating steps 3 to 5). This

186 search will only stop when i) the virtual buzzard has met its area requirements for rough-ground
187 (*rgr-area*) and moved back to the roosting site, or ii) it has not met these requirements and hence
188 left the area.

189

190 6. The search for meadow begins from the roosting site and happens in exactly the same way as that
191 for rough-ground (excepting, naturally, the changes to *mead-area* and to *mead-dist*). It stops when
192 i) the meadow resource needs (*mead-area*) have been met or ii) they have not been met and hence
193 the virtual buzzard left the area. When the meadow resource needs have been met the territory will
194 have been fully formed. Another virtual buzzard will then arrive at a random woodland patch which
195 is as yet undefended and try to establish a territory by following the exact same rules (steps 2 to 6).

196

197 7. The exhaustion of free woodland patches, which causes the model to stop, leads to the emergence
198 of maximum distribution and abundance in the landscape.

199

200 **5. *Main model assumptions***

201 The main assumptions of our model were that: i) the random selection of the woodland patch for
202 roosting does not lead to different maximum distribution and abundance than some other form of
203 colonisation; ii) the wild buzzard does not actively avoid any land-cover that does not contain a key
204 resource; iii) the key resource-containing categories of LCMGB of 1990 were perfectly mapped (an
205 assumption of RADA); iv) there is a proportional relationship between patch area and amount of
206 accessible resource (an assumption of RADA); v) wild buzzards defend only the patches that
207 provide them with the minimum amount of the needed resources.

208

209 **6. *Calibration***

210 Parameter values, calibration intervals, steps and references are shown in table 2. Parameterisation
211 was restricted to the forage search distances for rough-ground and meadow. To capture home-range

212 structure, we assessed the utilisation distributions from 30% to 80% outlines at 5% intervals,
213 because cores $> 80\%$ are associated with activities other than foraging, such as social interactions
214 [22]. Initial values were based on a previous study [25] and final values were those which
215 minimised the sum of the absolute differences between mean core% area of virtual and wild
216 buzzards across the eleven cores. Tests with up to 50 model runs per parameter value combination
217 showed 6 runs sufficed for obtaining reasonably stable results while considerably reducing
218 runtimes.

219

220 Table 2

221

222 ***7. Landscape change scenario***

223 Maps of landscape change scenarios represented the rural economy gradually shifting from meadow
224 to woodland, motivated by, inter alia, woodland's role in flood management, timber's value for
225 construction, and vegetarianism/veganism reducing the need for grassland to feed livestock [9–11].
226 The smallest economically viable plot for meadow conversion to woodland was considered to be 20
227 ha [18]. Scenarios represented 30%, 60% and 90% conversion of randomly chosen meadow plots
228 larger than 20 ha into woodland.

229

230 ***8. Output verification***

231 The model was assessed qualitatively and quantitatively with regards to producing virtual buzzards
232 with home-ranges with size, shape and pattern of overlap similar to wild buzzards. Virtual and wild
233 buzzard home-range cores and territories were plotted in a GIS to obtain three parameters of home
234 range structure relevant to defence of resource patches. Virtual buzzard pairwise home-ranges

overlaps, a proxy for their territorial behaviour and an emergent pattern in the model, were compared with those of wild buzzards using two-tailed tests [32].

237

238 **9. Sensitivity analysis**

Local (LSA) and Global Sensitivity Analysis (GSA) were performed. LSA used a modified version of the Morris screening method, which makes no assumptions about the model and uses individually randomised one-factor-at-a-time designs to assess the effects of changes in parameter values on outputs [33,34]. The modified Morris screening was used to assess the relative importance of rough-ground area and rough-ground forage search distance, and meadow area and meadow forage search distance, on each of six individual- and population-level model outputs: abundance, 80% home-range core overlap percentage, 40% home-range core area, 80% home-range core area, 40% home-range core perimeter, 80% home-range core perimeter (explanation of the modified Morris Screening method is presented in the TRACE document in SI). Parameter values for rough-ground forage search distance and area, and for meadow forage search distance and area, were varied around the reference values by, respectively, 70% and 67%, 67% and 67%. GSA was based on a full factorial design and aimed at assessing possible interactions between the two main parameters influencing abundance, namely meadow area and forage search distance; meadow area: min = 9.5 ha, max = 17.5 ha, step = 1ha, and meadow forage search distance: min = 800 m, max = 1600 m, step = 100 m.

254

255 **10. Output corroboration**

256 Predictions for maximum abundance were compared with estimates obtained via mark-resighting
257 and radio-corrected distance-transects carried out in 1995-96 [23]. The final spatial distributions of
258 home-ranges and territories were also visually compared to those of the sample of wild buzzards.

259

260 **Results**

261 *Individual-level predictions: home-range structure*

262 Home-ranges of virtual buzzards were similar to those of wild buzzards visually (figure 2) and
263 quantitatively (figure 3). The relative frequency distributions for size and perimeter of 80% convex
264 polygons for both virtual and wild buzzards were positively skewed, with close means, medians and
265 inter-quartile ranges. As calibration results indicate, the virtual buzzards' inner core (40% polygon),
266 which was associated most strongly to rough-ground, was also similar to that of wild buzzards
267 (figure S8). As with the wild birds, about 70-80% of virtual buzzards had compact resource-
268 associated cores in the richer meadow zones. The rest of the wild and virtual animals occurred
269 where rough-ground or meadow were thinly spread, for example due to another buzzard's territory,
270 an urban zone or a large patch of arable land being in the way. These formed 80% convex polygons
271 one order of magnitude larger than the more compact ones, which is a significant variation in terms
272 of possibilities for occupying space.

273

274 Figure 2

275

276 Figure 3

277

278 The collective territorial pattern of virtual buzzards, which was emergent in the model, was also
279 similar to that of wild buzzards (figure 3 and S4-S6). Again, this was true in terms of positive

280 skewness, means, medians and inter-quartile ranges, and overlap between neighbouring home-
281 ranges (Mann-Whitney U Test, two-tailed, pairwise, involving overlaps between 114 wild and 276
282 virtual buzzards and null hypothesis that there was no difference between the two samples yielded:
283 $W = 24548$, $p=0.219$). Thus, in addition to roosting on a woodland patch and defending the same
284 key resources, virtual buzzards also shared space with neighbours similarly to wild buzzards.

285
286 ***Population-level predictions: abundance and distribution within the 1994 landscape***

287 Mean maximum abundance over 100 runs was about 7% and 10% larger than mean abundance
288 based on Transect-counting or Mark-resighting, respectively (table 3 and S6-S7). The distribution
289 of virtual buzzards encompassed that of wild buzzards and extended to areas where they were not
290 tracked (figure S6).

291
292 Table 3

293
294 ***Population-level predictions: abundance and distribution within landscape change scenarios***

295 Predictions for 30%, 60% and 90% of meadow fields (of > 20 ha) being converted into woodland
296 were that the number of buzzard territories within the study region would decline non-linearly by
297 15%, 38% and 74%, respectively (table 3). The reason was primarily that, with reduction and
298 dispersion of meadow, the smaller cores that once abounded became unviable (figure 4).

299
300 Figure 4

301
302 ***Sensitivity analysis***

303 LSA showed the main parameter influencing abundance, and in an inverse way, was the
304 individual's meadow area requirement (figures S9-S10). Rough-ground area also inversely
305 influenced abundance, but much less strongly. Pairwise home-range core overlaps depended mainly

306 and inversely on how far a buzzard could search for meadow, though overall variability was less
307 than 7%. Home-range area and perimeter lengths of the inner and outer cores depended more
308 strongly on how much meadow the individual required, and how far it would go to find it, the latter
309 prevailing with regards to outermost core areas and perimeter lengths. We note that despite the
310 small effect on outputs of rough-ground area and forage search distance, these parameters were kept
311 because they refined results and made the model applicable to landscapes with greater variation in
312 structure.

313

314 **Discussion**

315 In the study area, mean virtual buzzard abundance (100 runs) was between seven and ten percent
316 larger than field estimates based on Transect-counting and Mark-resighting, respectively (table 3).
317 A few isolated places within the study area, corresponding to about five percent of its extent, were
318 not easily accessed during fieldwork for radio-tagging or population censusing, and the model
319 predicted they could accommodate buzzards. Discounting the number of buzzards predicted within
320 these areas reduces the difference between model and field estimates to roughly five percent, which
321 is within the uncertainty associated with each technique (table 3), and hence unlikely to be
322 biologically meaningful. We thus conclude that by 1995, at least, buzzards in the area had recovered
323 to maximum density.

324

325 When the landscape change scenarios were considered, buzzard abundance in the study area
326 decreased steeply and non-linearly with the increased conversion of meadow patches of
327 economically-viable size (> 20 ha) into woodland (table 3 and figure 4). As explained earlier, a
328 report from UK Centre for Ecology and Hydrology (UKCEH) showed that over the last 25 years
329 land uses in Great Britain and Northern Ireland have changed from arable (-0,3%) and, mainly,

grassland (-3,0%) to urban (+1,3%) and woodland (+2,0%) [8]. Therefore, in areas where buzzard numbers have built to maximum capacity, a loss of meadow is expected to have led to a decline in density. However, this decline is expected to have happened in only a few places as yet, because in most areas of lowland UK buzzard densities are still increasing.

Buzzard home-range structuring and territoriality

The question of what influences a buzzard's territory in lowland UK has been considered for over forty years, with hypotheses about the roles of resource accessibility, social excursions and territorial disputes [35]. The results here further corroborate our earlier analysis [15], which indicated that the territory consists of a patch of woodland for roosting and enough rough-ground and meadow to meet minimum requirements for hunting small mammals and invertebrates (figure 2). This fits with the interpretation that common buzzards follow a contractionist [36] or area-minimizing home-range strategy [37], where ranges are tightly shaped by resource dispersion. Other examples of animals with a similar home-range strategy are goshawks *Accipiter gentilis* [38], Blandford foxes *Vulpes cana* [39], some populations of spotted hyaenas *Crocuta crocuta* [36], African lions *Panthera leo* [40] and female black bears *Ursus americanus* [41]. Naturally, animals following this strategy are particularly affected by changes to landscape structure, as exemplified here (figure 4).

Model uncertainties and possible improvements

For distribution and abundance, uncertainty in prediction was associated mainly with i) the estimation of meadow area requirement and ii) how well the virtual buzzard's territorial behaviour represented that of the wild buzzard. The precision of the meadow area requirement depended on

the applicability of the assumptions that the LCMGB of 1990 was fully accurate and of there being a proportional relationship between patch area and resource accessibility, both of which depended to a large extent on the quality of home-range estimation and mapping [19,22]. In practice, omission error in the mapping of meadow would lead to underestimation of the minimum individual requirement and hence to overestimation of abundance, while commission error would have the opposite effect. The representation of territories, in its turn, was based on hypothesis testing using variants of the ABM that differed by how the virtual buzzard defended its key resources (figures S4-S5). In addition, calibration of forage search distances may have led to overfitting that could be minimised, and the model made more general, with use of energy budgets [42,43].

362

Predictions for the change scenarios did not consider possible functional relationships with other species [44]. For example, large proportional increases in woodland area may lead to more (re-introduced) goshawks, which compete with buzzards for woodland and edge prey and, being also a predator of buzzards, may deter buzzards from foraging for worms in meadow near woodland [45]. Such a further reduction in buzzard density would stem from a mechanism not included in our model.

369

370 *Anticipation of animal population patterns in changing landscapes*

Resource Selection Functions (RSF) seem to be the most popular method to predict animal distribution and abundance in the geographical space of a real landscape. A RSF can predict these population patterns from correlations between a wide variety of data about animal presence, e.g. spoor or GPS tracking, and for resources or conditions, e.g. land-cover or altitude [46,47]. Important assumptions of a RSF are that 1) the animal population is at equilibrium density or following an ideal free distribution when the calibration data are collected, 2) abundance does not

depend on factors other than resources, and 3) the availabilities of the resources in the calibration and extrapolation landscapes are similar [46]. An example of when assumptions (1-2) would not have been reasonable was shown with an ABM for oystercatchers in the Exe estuary, UK. Mortality was found to be influenced by interference competition only after a certain density threshold, so a RSF built using data collected when density was below this threshold would overestimate maximum abundance by a considerable margin [43]. Additionally, when the resources are found within a landscape category that is being impacted by human action, e.g. meadow for buzzards being replaced by woodland, assumption (3) may be hard to meet and therefore extrapolations to future landscapes may be problematic. Thus, the assumptions underlying a RSF can restrict applicability to certain situations that may be particularly important for conservation, such as when an animal population is below equilibrium density owing to endangerment or recurrent perturbations, or when the aim is to assess the impact of landscape change on wildlife.

ABM offers greater flexibility by allowing for the explicit representation of an ecological mechanism that connects animal space use with landscape structure — fundamentally, the procurement by individual organisms of the resources needed to survive and breed [26,42,48,49]. However, carrying out the fieldwork required to identify and quantify individual animals' resource needs has often been challenging. Thus, in pioneering landscape-explicit ABM resource-based parameters were assumed, as for red and grey squirrels *Sciurus vulgaris* and *S. carolinensis* [50], or four small mammal species in the UK [51]. Alternatively, such parameters were supported by field-data collected over decades, e.g. oystercatchers *Haematopus ostralegus*, UK [52], skylarks *Alauda arvensis* in Denmark [53] and river salmonids in California, USA [54], sometimes across thousands of kilometres squared, e.g. grey wolves *Canis lupus* in the Italian alps [55], African elephants *Loxodonta africana* in the Kenya-Tanzania border [56], and tigers *Panthera tigris* in Nepal's Chitwan National Park [57].

403 The strength of the ABM approach we applied to buzzards comes from having estimated the virtual
404 animals' resource needs from wild animals using RADA. The use of remote animal tracking and
405 satellite mapping of the resources has the potential to allow for more efficient estimation of the
406 ABM parameters, and to considerably increase the range of species that can be simulated [58–60].
407 For example, the rapid recent reduction in size of GPS tags has been revealing the intricate home-
408 ranges of small birds, such as of the European nightjar *Caprimulgus europaeus* that weighs around
409 60 g [61]. In turn, populations of a single tree species have been mapped on the basis of variation in
410 crown shape and phenology with very high-resolution ($< 1\text{m}$) satellite imagery [62,63], while land-
411 cover mapping with spatial resolution suitable for detailed analysis of animal resource use (10-30m)
412 is increasingly available for many countries, continents and even the entire planet [8,64–68].
413 Importantly, RADA has worked with small sample sizes, as shown by results for data gained in
414 single years during 10-day tracking sessions also for 15 red and 17 grey squirrels, and for
415 contractionists or area-minimising home-range strategists it is expected to work even when the
416 population is below equilibrium density [17]. Additionally, citizen-scientists can get involved in
417 tracking or mapping [69], thus facilitating bottom-up management of landscapes and species, which
418 across 34 mainly European local studies was found to have more influence than top-down
419 management on sustainability of local biodiversity and ecosystem services [70]. Indeed, IUCN
420 nowadays recommends planning 'Nature-based solutions' at the landscape scale and considering
421 local knowledge [71].

422

423 Our results have shown that replacing meadow with trees is likely to reduce the buzzard density in
424 the area we studied. Moreover, we can apply the model to other areas of the UK if land managers
425 want to consider the wider effects of planting trees on a prominent and protected species, or develop
426 similar models of other species tracked in appropriately mapped areas. Anticipating that a crucial
427 population will prosper, or an agricultural pest collapse, can help harmonise economic development
428 with animal conservation and ecosystem service provision. We thus hope that the breadth,

429 efficiency and simplicity of the modelling approach used here may contribute to addressing the
430 more general conservation paradox that “we are not limited by lack of knowledge but failure to
431 synthesize and distribute what we know” [72].

432

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437

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443

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620 [cover_mapped_in_10_m_resolution#.YFIVQ8xfaR8.link](https://www.esa.int/ESA_Multimedia/Images/2020/03/Europe_land-cover_mapped_in_10_m_resolution#.YFIVQ8xfaR8.link).
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633 **Tables**

634 Table 1. Buzzard RADA-ABM entities, state variables, units and descriptions. Composite names of
635 virtual buzzard state variables are separated by a dash, and of the resource maps and the
636 pseudorandom number generator by an underscore.

Entity	State Variable	Unit	Description
Pre-breeding buzzard	name	integer	ID
	my-roost	pixel	Defended woodland pixel
	my-rgr	pixel	Defended rough-ground pixels
	my-mead	pixel	Defended meadow pixels
	X	m	Eastings of resource pixels forming territory
	Y	m	Northings of resource pixels forming territory
Resource	map_cat	integer	Map category ID of pixel in land-cover map
	resource	string	Map category ID of pixel in buzzard resource map
	available?	boolean	Whether a resource pixel is free or defended
	searched?	boolean	Whether a resource pixel has had its free same-resource neighbouring pixels searched
Global	rgr-area	integer	Area of rough-ground required in inner range core (RADA)
	rgr-dist	m	Constraint on distance from roosting-site for rough-ground searches (but not for rough-ground defence)
	mead-area	integer	Area of meadow required in outer core (RADA)

mead-dist	m	Constraint on distance from roosting-site for meadow searches (but not for meadow defence)
resource_data	pixel	LCMGB 1990 or land-cover change scenario to be translated into buzzard resource map
m_1990	pixel	Buzzard resource map; translation of the LCMGB
s_30%	pixel	Scenario 1 (S1): 30% of economically-viable meadow (>20ha) turned into woodland
s_60%	pixel	Scenario 2 (S2): 60% of economically-viable meadow (>20ha) turned into woodland
s_90%	pixel	Scenario 3 (S3): 90% of economically-viable meadow (>20ha) turned into woodland
map_eastings	m	E-W resource map extent
map_northings	m	N-S resource map extent
seed	integer	User-defined number ('seed') for pseudorandom number generator
seed_on	on/off	If 'on', pseudorandom number generator begins with user-defined seed, making run fully deterministic

638 Table 2. Model parameters (state variables), value and reference for value, and interval and step
639 used in calibration. To establish a home-range in the study area, the virtual buzzard needed a
640 tree to roost (woodland) and to search for enough rough-ground and meadow (area
641 parameters) to meet requirements for small mammals and invertebrates.

Parameter	Value	Interval	Step	Source
my-roost	0.06 ha	-	-	Data (25x25m pixel)
rgr-area	0.56 ha	-	-	RADA
mead-area	13.5 ha	-	-	RADA
rgr-dist	500 m	300-500	50	Data + Calibration
mead-dist	1200 m	1150-1350	50	Data + Calibration

642

643 Table 3. Abundances of buzzards in the 1990s landscape (UK), with scenarios of (S1) 30%, (S2)
644 60% and (S3) 90% conversion of meadow into woodland (100 runs each). For comparison,
645 field-based estimates using Transect-counting (*T*) and Mark-Resighting (*M-R*) were obtained
646 from surveys carried out during 1995-6 [23].

	<i>T</i>	<i>M-R</i>	UK	S1	S2	S3
Abundance (mean)	256	250	275	235	170	71
95% CI	152-435	82-417	274-276	234-236	169-171	70-72
Range (min-max)	-	-	264-287	222-245	158-181	63-77

647

648 **Figures captions**

649 Figure 1. High-level model algorithm.

650

651 Figure 2. Virtual and wild buzzards in lowland UK. (A) Nuclear area of a virtual buzzard's home-
652 range, formed by roosting site (yellow) and nearby defended patches of rough-ground (purple) and
653 meadow (orange). In each of (B-D), one virtual and one wild buzzard occupy adjacent home-ranges
654 of similar size and shape as defined by 80% convex polygons. Background maps in (A-C) are
655 recent Google Satellite (<1 m) [73] and (D) is an Open Street Map [74] as often used to inform
656 policy. Buzzards' data projected using 1936 British National Grid (EPSG 27700), with location
657 resolution: virtual = 25 m; wild = 100 m.

658

659 Figure 3. Comparison of wild and virtual buzzards' relative frequency distributions for home-range
660 core area, perimeter, and pairwise overlaps of 80% range cores (as proxy for territorial spacing),
661 with sample size (N), mean, median and inter-quartile range (IQR). To improve visibility, the
662 largest home-range of a wild buzzard, which was 1270 ha, was omitted. Core area was calibrated
663 based on mean values only, not the shape of the distribution, and neither perimeter nor overlap were
664 subject to calibration (See Calibration in SI).

665

666 Figure 4. Partial view of predictions for common buzzard maximum abundances and distributions:
667 (A) landscape at the time of tracking, and conversion of (B) 30%, (C) 60% and (D) 90% of
668 meadows larger than 20 ha into woodland, for timber production. Note that roosts (dots) can lie
669 outside core foraging ranges, but not outside the (dashed) study area. Data projected using 1936
670 British National Grid (EPSG 27700).

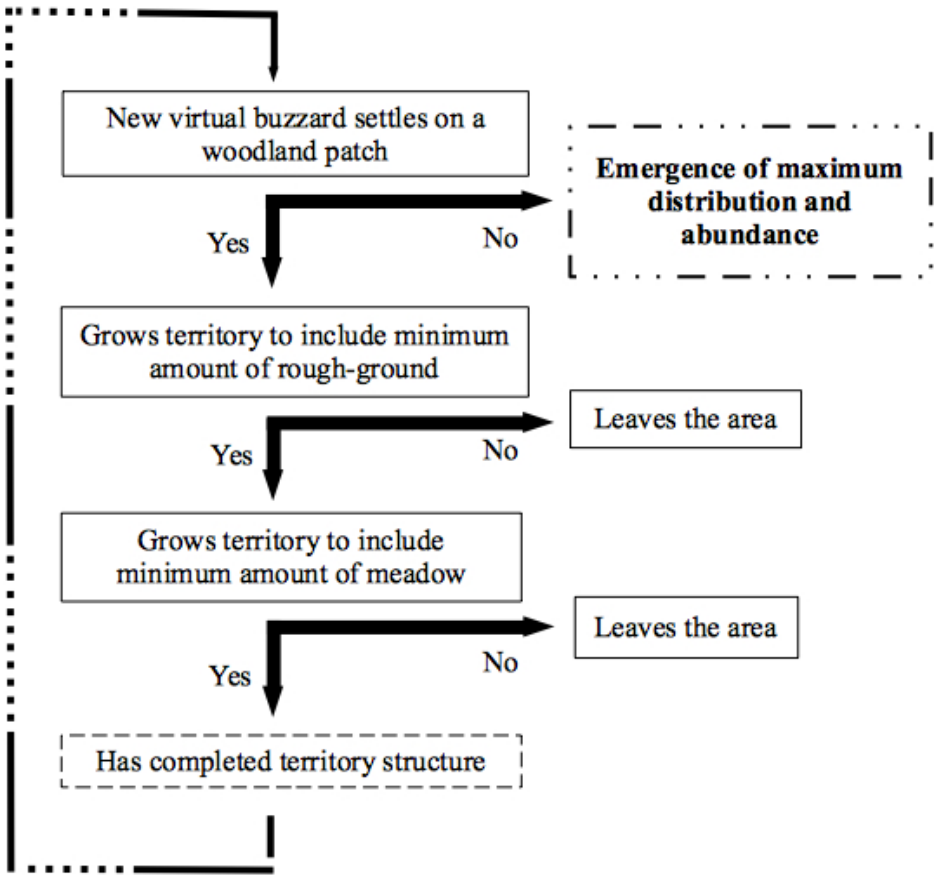


Figure 1. High-level model algorithm.

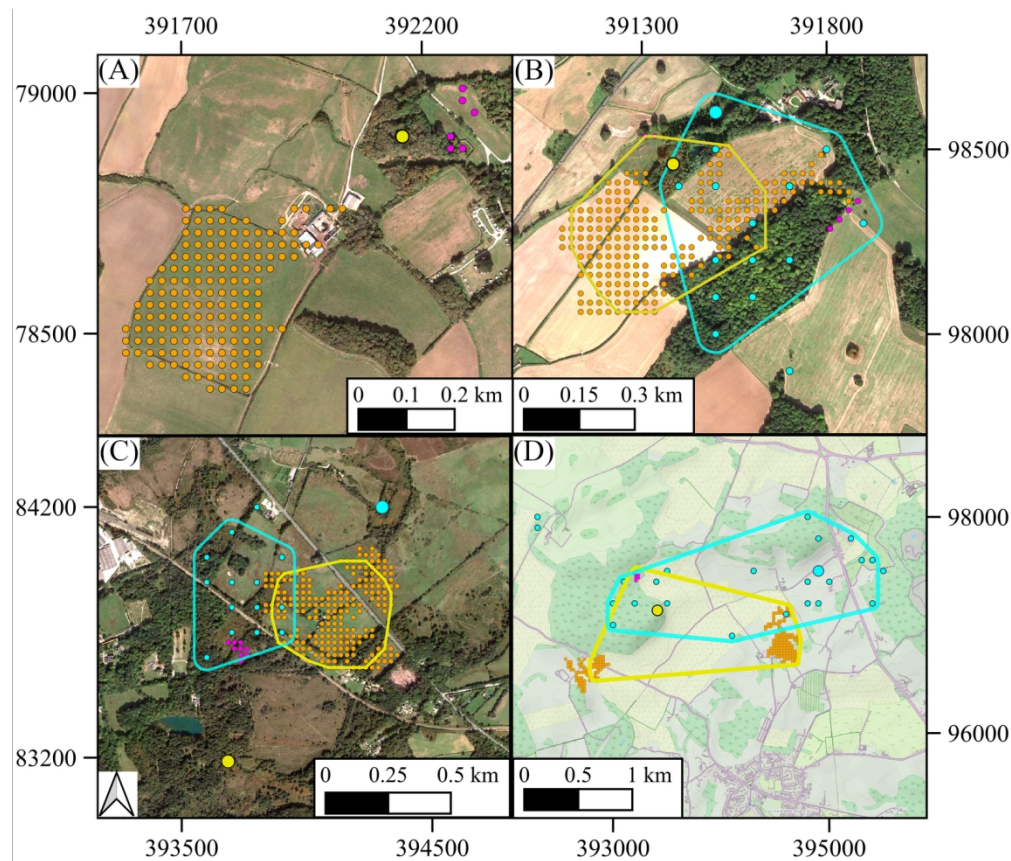


Figure 2. Virtual and wild buzzards in lowland UK. (A) Nuclear area of a virtual buzzard's home-range, formed by roosting site (yellow) and nearby defended patches of rough-ground (purple) and meadow (orange). In each of (B-D), one virtual and one wild buzzard occupy adjacent home-ranges of similar size and shape as defined by 80% convex polygons. Background maps in (A-C) are recent Google Satellite (<1 m) [73] and (D) is an Open Street Map [74] as often used to inform policy. Buzzards' data projected using 1936 British National Grid (EPSG 27700), with location resolution: virtual = 25 m; wild = 100 m.

142x121mm (300 x 300 DPI)

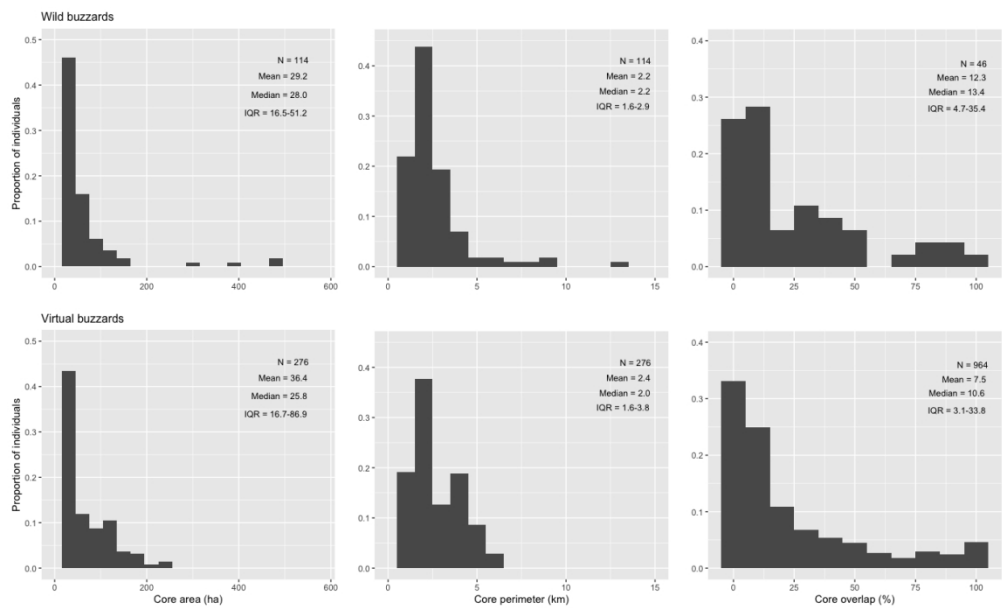


Figure 3. Comparison of wild and virtual buzzards’ relative frequency distributions for home-range core area, perimeter, and pairwise overlaps of 80% range cores (as proxy for territorial spacing), with sample size (N), mean, median and inter-quartile range (IQR). To improve visibility, the largest home-range of a wild buzzard, which was 1270 ha, was omitted. Core area was calibrated based on mean values only, not the shape of the distribution, and neither perimeter nor overlap were subject to calibration (See Calibration in SI).

488x294mm (72 x 72 DPI)

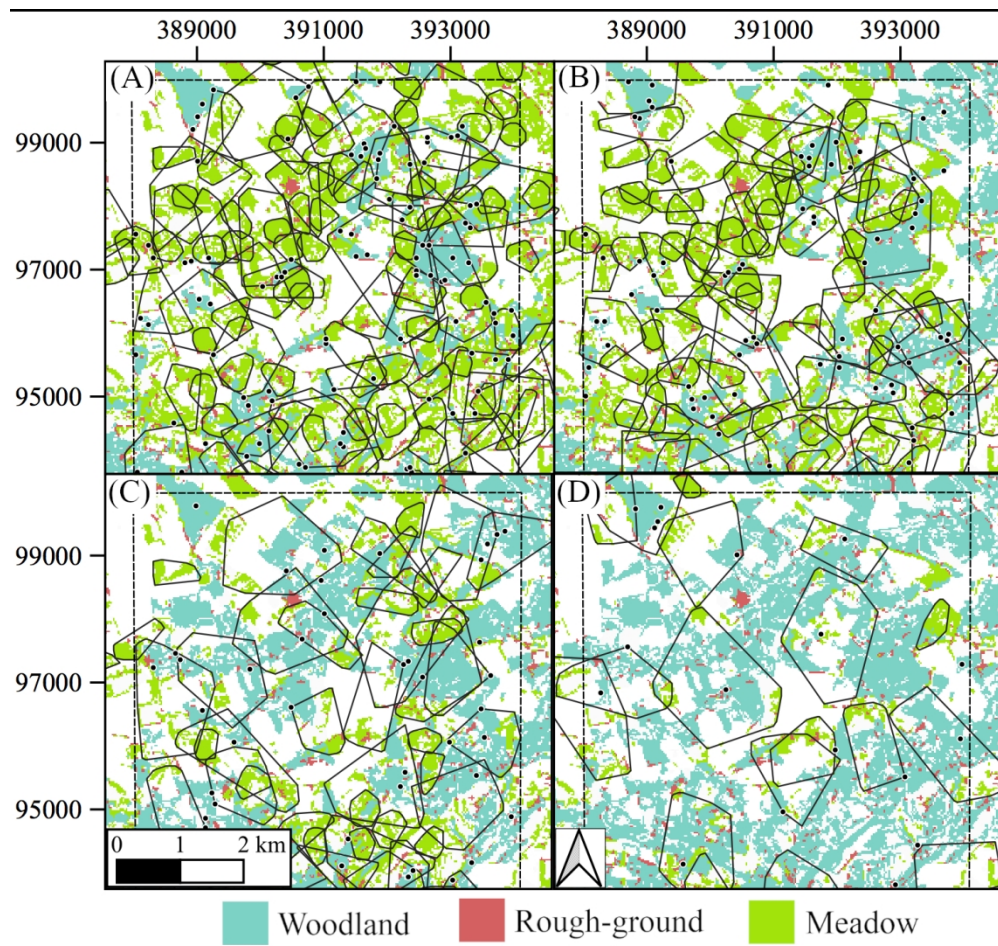


Figure 4. Partial view of predictions for common buzzard maximum abundances and distributions: (A) landscape at the time of tracking, and conversion of (B) 30%, (C) 60% and (D) 90% of meadows larger than 20 ha into woodland, for timber production. Note that roosts (dots) can lie outside core foraging ranges, but not outside the (dashed) study area. Data projected using 1936 British National Grid (EPSG 27700).