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2 **THE PERSISTENCE OF *Lasius flavus* ANT-HILLS AND THEIR INFLUENCE ON BIODIVERSITY IN**
3 **GRASSLANDS**

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10 **ABSTRACT**

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12 The allogenic ecological engineer *Lasius flavus* (F.) is a keystone species in many
13 grasslands, increasing their heterogeneity, creating microhabitats for many other species
14 and considerably influencing soil ecology between the mounds. John Pontin mapped ant-
15 hills built by *Lasius flavus* at Wytham Woods in 1955-1962. They were mapped again 62
16 years later. The majority were still in their original positions. Ant-hills have a characteristic
17 flora and fauna. A list is provided of those animal species strongly influenced by ant-hills,
18 including those which might be absent from mature grasslands if ant-hills were absent.
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20 **INTRODUCTION**

21
22 Mounds built by the yellow meadow ant *Lasius flavus* (F.) are characteristic features in
23 many grazed grasslands in the UK and northern Europe (Pontin, 1961; King, 1977; Pontin,
24 2005; Seifert, 2018). They often bear a distinct flora (Table 1), and support fauna which
25 would not exist in the absence of this ant species (Table 2). In mature grasslands the ant-hill
26 surfaces may make up 5-24% of the total surface area and the soil accumulated by the ants
27 may weigh up to 150-240 tonnes/ha. The workers forage beneath the surrounding
28 grassland, in particular for the honeydew secreted by the root aphids on which they
29 depend. Adding the numbers in the mounds to the numbers beneath the surrounding
30 grassland, they reach mean worker densities of 6,122/m² (95% confidence limits 9206-3038
31 workers/m²) - mean of ten studies 1961-2018 (e.g. Odum & Pontin, 1961 at this site; Pontin,
32 1978; Langley, 1986; Wright, 1990).

33 It seems likely that ant-hills exist in exactly the same places for centuries; on the Porton
34 Ranges, Hampshire the most rapidly-growing mounds increase in volume by a litre a year
35 (Wells *et al.*, 1976; King, 1981a). This paper documents the persistence of many ant-hills
36 after 62 years, the longest for which an ant-hill population has been thoroughly
37 documented. The plot on the Bowling Alley, Wytham Woods, Oxfordshire (SP 46440 07439)
38 in which the ant-hills were mapped by John Pontin (Pontin, 1958, 1961, 1963) was relocated
39 precisely in February 2018, on the basis of the current patterns of mounds and tor grass
40 *Brachypodium rupestre* (formerly recorded as *B. pinnatum*).
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42 **METHODS**

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44 Once the margins of the 222m² plot (Fig. 1) had been established the current positions of
45 the ant-hill summits were mapped by triangulation in relation to the corners and the
46 positions of pines and hawthorns. Pontin's 1962 map (Pontin, 1963) and the 2018 map were
47 then compared (Fig. 1). Ant-hill volumes ($V = \pi h(3a^2+h^2)/6000$ in litres) and surface areas

48 (SA = $\pi(a^2+h^2)$ /10000 in square metres) were estimated as if they were spherical caps using
 49 established methodology for estimating their heights (h) and radius (a) in cm (King 1981a,
 50 2018).



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53 Fig. 1. Pontin's plot on the Bowling Alley, Wytham Woods (March 2018).

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55 The list of angiosperms and bryophytes more or less confined to ant-hills at Wytham Woods
 56 (Table 1) is based on over 50 years of field experience there, and 22 days of sampling in
 57 2018. The list of animal species particularly influenced by *Lasius flavus* ant-hills is compiled
 58 from the literature. For example Wright (1990), comparing the numbers of rabbit droppings
 59 on and off ant-hills in 20 plots at Old Winchester Hill NNR, Aston Rowant NNR and Martin
 60 Down NNR found a mean maximum of 41.2 droppings on ant-hills (95% confidence limits
 61 33.3-49.0) and a mean maximum of 2.4 droppings on equivalent areas of grassland close by
 62 (95% confidence limits 1.4-3.4).

63 Nomenclature follows Stace (2019) for angiosperms and Atherton, Bosanquet & Lawley
 64 (2010) for bryophytes.

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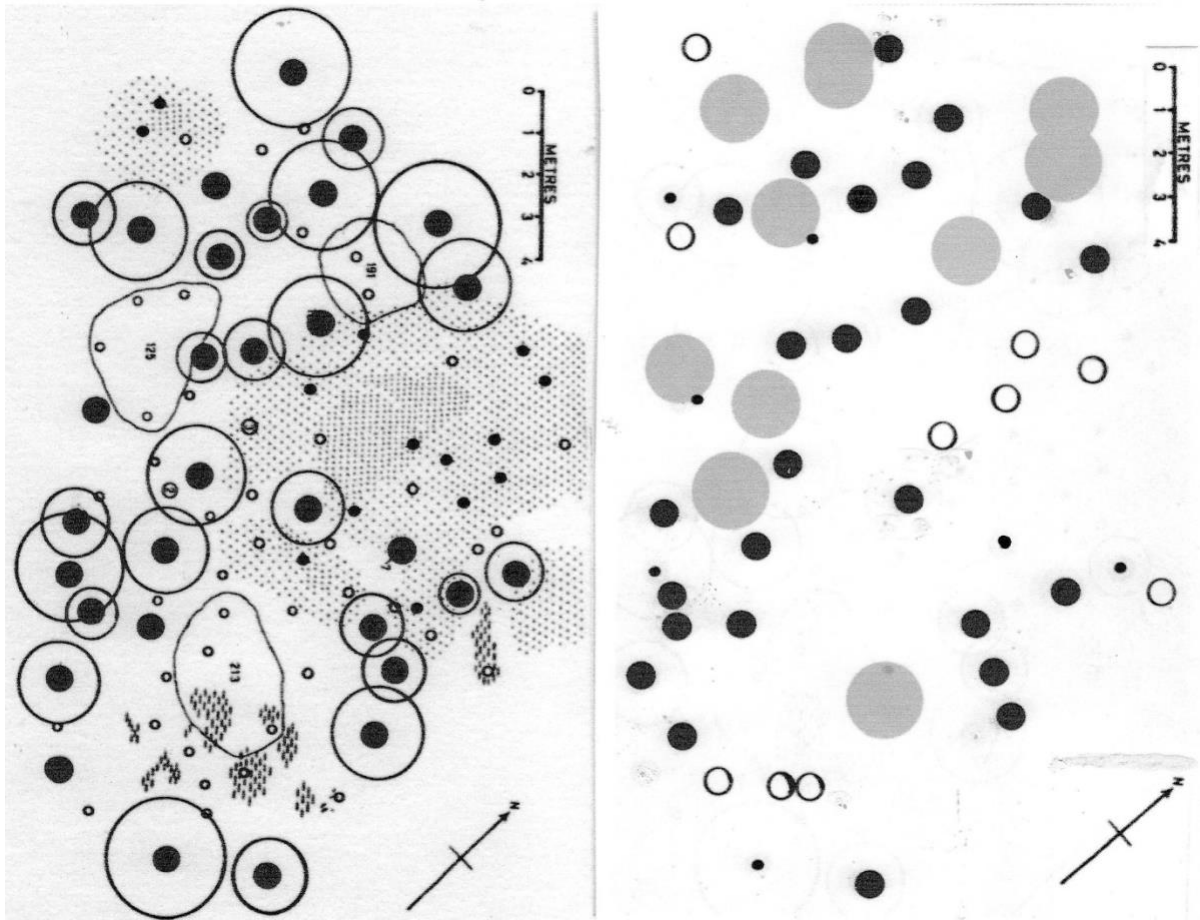
66 RESULTS

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68 Of the 31 *L. flavus* ant-hills which had produced queens in 1962, all of which had been
 69 present in 1956, 26 were still prominent in 2018 (Fig. 2), although only fourteen of these
 70 appeared to contain *L. flavus* colonies 56 years later. Ten new ant-hills had become
 71 established.

72 The current height of 57% of the 21 mounds exceeds their radius. The average ratio
 73 of height to radius is 2.13 (95% confidence limits 1.95-2.24). In 1958 none of the mounds
 74 exceeded 25 cm in height; 17 of the remaining mounds are now taller than this. Their
 75 volume is 266,000 l/ha, or perhaps 200,000 kg/ha (200 tonnes/ha).

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81 Fig. 2. Bowling Alley, Wytham Woods.

82 A. Map of *Lasius flavus* ant-hills in 1962, adapted from Pontin (1963). Large black dots show
83 those producing alate queens. Circles show presumed territory areas. Small black dots show
84 colonies eliminated after invasion of tor grass *Brachypodium rupestre*.85 B. Map of same area in 2018. Large black dots show prominent ant-hills. Small black dots
86 show ant-hills present in 1962 which have since disappeared. Open circles show ant-hills not
87 present in 1962. Large grey circles show hawthorn shrubs *Crataegus monogyna*.

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89 *Lasius flavus* ant-hills increase the plant species richness of a grassland, in particular,
90 because some winter annuals and acrocarpous bryophytes are often confined to them
91 (Table 1). In UK calcareous grasslands they support vegetation categorised as CG7 in the
92 National Vegetation Classification (Rodwell, 1992) whilst the surrounding grassland may be
93 in CG2-6 (King, 1977). In acidic grasslands ant-hills in U1 are frequently surrounded by
94 grasslands in U4 (King, 1981b; Rodwell, 1992). They provide distinct island microhabitats
95 within grasslands, supporting small-scale meta-populations of plant species and
96 invertebrates which might otherwise become locally extinct (King, 2006). In particular, the
97 annual creation of surface-heaped soil provides bare soil which would not otherwise exist
98 on this scale. An estimate by the author in summer at 16 sites across the southern UK (per
99 cent cover on 130 ant-hills) put bare soil at 9.2% of the ant-hill soil surface (95% confidence
100 limits 7.0-14.6%). Those animal species which are particularly influenced by *L. flavus* or
101 depend on its ant-hills for survival are listed in Table 2.

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Table 1. Plant species more or less restricted to ant-hills in Wytham Woods' grasslands.

Angiosperms, particularly winter annuals: Parsley-piert (*Aphanes arvensis*), Thyme-leaved sandwort (*Arenaria serpyllifolia*), Soft-bromes (*Bromus lepidus/hordaceus ssp.hordaceus*), Common mouse-ear (*Cerastium fontanum*), Dwarf mouse-ear *C. pumilum*, Common whitlowgrass (*Erophila verna*), Cut-leaved crane's-bill (*Geranium dissectum*), Three-nerved sandwort (*Moehringia trinervia*), Early forget-me-not (*Myosotis ramosissima*), Small-flowered buttercup (*Ranunculus parviflorus*), Rue-leaved saxifrage (*Saxifraga tridactylites*), Common chickweed (*Stellaria media*), Lesser trefoil (*Trifolium dubium*), Wall speedwell (*Veronica arvensis*).

Bryophytes, *Bryum caespitium* (frequent), *B. capillare*, *B. (klinggraeffi?)i*, *Bryum rubens*, *B. ruderale* (frequent), *Ceratodon purpureus*, *Didymodon fallax*, *Encalypta vulgaris*, *Ephemerum recurvifolium*, *Fissidens taxifolius*, *Pleuridium (acuminatum/subulatum?)*, *Tortula lanceola*.

Table 2. Animal species particularly influenced by the presence of *Lasius flavus*, including myrmecophiles.

| SPECIES | SPECIES GROUP | COMMENTS | REFERENCES |
|--|------------------|------------------------|-----------------------|
| <i>Oryctolagus cuniculus</i> (L.) | Rabbit | Preferential dunging | 39 |
| <i>Picus viridis</i> (L.) | Green Woodpecker | Ant feeder in winter | 1, 16, 18 |
| <i>Pyrhhorax pyrrhorax</i> (Tunstall) | Chough | Anting, predator | 6 |
| <i>Perdix perdix</i> (L.) | Grey partridge | Dust bathing, predator | 28 |
| <i>Anoecia corni</i> (Fabricius) | Hemiptera | Mutualism; farmed | 17, 19, 22, 26 |
| <i>Anoecia furcata</i> (Theobald) | Hemiptera | Mutualism; farmed | 17, 22, 26 |
| <i>Anoecia pskovika</i> Mordvilko | Hemiptera | Mutualism; farmed | 22, 26 |
| <i>Anoecia zirnitsi</i> Mordvilko | Hemiptera | Mutualism, farmed | 22, 39 |
| <i>Baizongia pistaciae</i> (L.) | Hemiptera | Mutualism; farmed | 17, 22, 26 |
| <i>Forda formicaria</i> (von Heyden) | Hemiptera | Mutualism; farmed | 17, 19, 22, 25, 26 |
| <i>Forda marginata</i> (Koch) | Hemiptera | Mutualism; farmed | 9, 17, 22, 26 |
| <i>Geocica setulosa</i> (Passerini) | Hemiptera | Mutualism; farmed | 17, 22, 26 |
| <i>Geocica utricularia</i> (Passerini) | Hemiptera | Mutualism; farmed | 9, 17, 22, 25, 26, 39 |
| <i>Neotrama caudata</i> del Guercio | Hemiptera | Mutualism, farmed | 22, 25, 39 |
| <i>Tetraneura ulmi</i> (L.) | Hemiptera | Mutualism; farmed | 9, 17, 19, 22, 25, 26 |
| <i>Trama rara</i> Mordvilko | Hemiptera | Mutualism; farmed | 22 |
| <i>Trama troglodytes</i> von Heyden | Hemiptera | Mutualism; farmed | 17, 22, 26 |
| <i>Claviger testaceus</i> (Preysslner) | Coleoptera | Myrmecophile | 5 |
| <i>Platyarthrus hoffmanseggii</i> (Brandt) | Isopod | Trash dumps | 38 |
| <i>Zygaena purpuralis</i> (Brunnich) | Burnet moth | Oviposition/Larva | 33 |
| <i>Polyommatus icarus</i> (Rottemburg) | Common blue | Oviposition/Larva | 7 |
| <i>Polyommatus coridon</i> (Rottemburg) | Chalkhill blue | Larva/pupa | 7 |

| | | | |
|-------------------------------------|--------------------------|-------------------|----|
| Hesperia comma (L.) | Silver spotted skipper | Pupa | 34 |
| Corthippus brunneus (Thunberg) | Common Field Grasshopper | Oviposition (x28) | 30 |
| Corthippus parallelus (Zetterstedt) | Meadow Grasshopper | Oviposition (x14) | 30 |
| Ateleura formicaria von Heyden | silverfish | Myrmecophile | 21 |
| Microdon spp. eg devius (L.) | Hoverfly | Larva/pupa | 37 |
| Antennophorus pubescens Wasmann | Mite | Parasite | 8 |
| Trachyuropoda bostocki (Michael) | Mite | Myrmecophile | 3 |
| Urodiscella wasmanni (Kneissl) | Mite | Myrmecophile | 3 |
| Oplitis minimus (Berlese) | Mite | Myrmecophile | 3 |
| Urotrachys formicaria (Lubbock) | Mite | Myrmecophile | 3 |

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DISCUSSION

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The Bowling Alley may have been grassland for centuries (King, 2018). Charles Elton's diaries (Kirby, 2016) and Pontin's papers (Pontin, 1961,1963) suggest that it was short rabbit-grazed grassland from 1945-1955. The first myxomatosed rabbit was seen in September 1955. Rabbit disappearance led to dominant tor grass a few years later. The initial response of *L. flavus* to shading is to build its mounds more rapidly. This has been proved experimentally (Blomqvist *et al.*, 2000). The introduction of scrub clearance and grazing in about 1969, and occasional grazing and shrub removal subsequently, probably allowed the ant colonies to survive, with the consequence that unusually, many have a height exceeding the radius (Fig. 3).



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136 Fig. 3. One of Pontin's original ant-hills, containing an ant colony and about 44 cm high
137 (March 2018).

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139 It seems unlikely that any of these ant-hills has been continuously occupied. Although new
140 colonies are often founded by groups of queens, the queens have a limited life span in the
141 field, likely to be far less than the maximum (23 years) observed in the laboratory (Prescott,
142 1973). It is likely that colonies die when the queen dies, but that the bare soil on top is ripe
143 for invasion by newly-fertilised queens after the nuptial flight, particularly at this site, where
144 up to 410 queens can be produced annually by a single colony (Pontin, 1963). This is
145 probably why the summits of some of the ant-hills are not exactly in the positions recorded
146 by Pontin, or now have two summits.

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148 Grasslands with ant-hills are two-tone habitats; when recording in grasslands, it is important
149 to record whether or not sampled insects are associated with ant-hills, particularly because
150 the mounds increase the range of aspects, soil temperatures, soil nutrient and water
151 contents. In many grasslands they provide an overall cover of 1-3% bare soil, annually
152 replenished.

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155

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