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Published in:
Journal of Applied Ecology

DOI:
[10.1111/1365-2664.13647](https://doi.org/10.1111/1365-2664.13647)

Print publication: 01/08/2020

Document Version
Publisher's PDF, also known as Version of record

[Link to publication](#)

Citation for published version (APA):

Malm, L. E., Pearce-Higgins, J. W., Littlewood, N. A., Karley, A. J., Karaszewska, E., Jaques, R., Pakeman, R. J., Redpath, S. M., & Evans, D. M. (2020). Livestock grazing impacts components of the breeding productivity of a common upland insectivorous passerine: Results from a long-term experiment. *Journal of Applied Ecology*, 57(8), 1514-1523. <https://doi.org/10.1111/1365-2664.13647>

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Livestock grazing impacts components of the breeding productivity of a common upland insectivorous passerine: Results from a long-term experiment

Lisa E. Malm^{1,2}  | James W. Pearce-Higgins^{3,4}  | Nick A. Littlewood^{2,5}  |
 Alison J. Karley⁶  | Ewa Karaszewska⁶ | Robert Jaques^{3,6} | Robin J. Pakeman²  |
 Stephen M. Redpath⁷  | Darren M. Evans¹ 

¹School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, UK; ²The James Hutton Institute, Aberdeen, UK; ³British Trust for Ornithology, The Nunnery, Thetford, UK; ⁴Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK; ⁵Department of Rural Land Use, SRUC, Aberdeen, UK; ⁶The James Hutton Institute, Dundee, UK and ⁷Institute of Biological & Environmental Sciences, University of Aberdeen, Aberdeen, UK

Correspondence

Lisa E. Malm
 Email: malm.lisa@outlook.com

Funding information

Macaulay Development Trust; British Trust for Ornithology; University of Hull; Newcastle University; Strategic Research Programme; Scottish Government's Rural and Environment Science and Analytical Services Division; James Hutton Institute

Handling Editor: Marc-André Villard

Abstract

1. The intensity of pastoral management in areas of High Nature Value farming is declining in some regions of Europe but increasing in others. This affects open habitats of conservation concern, such as the British uplands, where bird species that benefit from low-intensity grazing may be most sensitive to such polarization. While experimental manipulations of livestock grazing intensities have improved our understanding of upland breeding bird responses in the short term, none have examined the long-term impacts of altered management on reproductive success.
2. Using a replicated landscape-scale experiment that started in 2003, we investigated the effects of four grazing treatments (intensive sheep; low-intensity sheep; low-intensity mixed sheep and cattle; and no grazing) on the breeding productivity of meadow pipits *Anthus pratensis*, the most common upland passerine. Surveys were carried out systematically during early (2003 and 2004) and late (2015 and 2016) sampling periods of the experiment to compare the short- and long-term effects of grazing treatments on breeding density and productivity of pipits specifically, but also on the overall bird community.
3. Pipit breeding density was lowest under low-intensity sheep grazing while the highest egg-stage nest survival was observed in the same treatment, although no significant treatment effects were detected on overall nest survival or fledgling output. There were no significant differences in treatment effects between the sampling periods on any breeding variable, but overall nest survival was lower in the later sampling period across all treatments.
4. Breeding bird species richness differed between treatments in the later sampling period, with highest species richness in the ungrazed treatment.

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5. *Synthesis and applications.* Livestock grazing management can have different outcomes for different upland birds. Our results showed that, with time, meadow pipit breeding productivity tended to be higher when sheep grazing intensity was reduced and/or mixed with cattle, and lower when livestock were removed, but not significantly so. Removal of grazing, however, can significantly increase bird species richness. The long-term experiment showed an overall decline in fledglings regardless of grazing treatments, potentially a result of increased predator numbers harboured by nearby developing woodland, highlighting the importance of considering wider landscape processes in grazing management decisions.

KEYWORDS

agriculture, avian biology, grasslands, meadow pipit, moorland, nest survival, predation, temporal change

1 | INTRODUCTION

One third of farmland in the European Union (EU) consists of permanent grasslands. However, the proportion of livestock fed through natural grazing is decreasing in the majority of European countries, and in many countries outside Europe (van den Pol-van Dasselaar, de Vliegheer, Hennessy, Isselstein, & Peyraud, 2015). As a result, more polarized management (i.e. intensification or abandonment) is anticipated in traditionally pastoral landscapes, of which many are of High Nature Value (Meiner & Bas, 2017). After decades of concerns about unsustainably high levels of grazing (Fuller & Gough, 1999), new concerns regarding under-grazing are emerging (IEEP, 2004).

Fuller, Gillings, Lauder, and Crowe (2013) found that bird species in upland habitats in Britain and Ireland have shown the strongest range contractions, during a 40-year period, compared to birds in other habitat types. Some population declines occurred alongside increases in livestock densities since the mid-20th century (Fuller & Gough, 1999). However, many species, particularly ground-nesting birds (Sullivan, Newson, & Pearce-Higgins, 2015), are still declining in abundance, despite lower sheep densities in some parts of the British uplands in recent years (Hayhow et al., 2017).

Livestock grazing intensity can affect ground-nesting, insectivorous birds through a number of mechanisms. Firstly, livestock may have a direct impact on demographic parameters, for example by trampling or preying on nests and chicks (Jarrett, Calladine, Wernham, & Wilson, 2017). Secondly, livestock may alter vegetation structure by their effect on sward height and density. This can not only alter the suitability of the habitat for different species, thus affecting bird settlement patterns (Loe et al., 2007), but may also alter the abundance and/or availability of their prey (Buchanan, Grant, Sanderson, & Pearce-Higgins, 2006; Dennis et al., 2008). Food availability is a function of both prey abundance and accessibility. For example, ground-foraging, insectivorous birds have been shown to prefer shorter vegetation with high arthropod abundance and accessibility, rather than simply high arthropod abundance (Douglas, Evans, & Redpath, 2008; Pearce-Higgins & Yalden, 2003). Thirdly, changes in vegetation structure may also affect the visibility and

hence vulnerability of nests to predators (Homberger, Duplain, Jenny, & Jenni, 2017). Moreover, predators may increase as a result of improved habitat suitability and/or higher population densities of other prey, such as small mammals (Evans et al., 2015). In the longer term, changes in grazing pressure, or complete removal of livestock, may alter the composition of vegetation, particularly the ratio of shrubs to sedges and grasses (Fuller & Gough, 1999), with further impacts on the abundance of bird species (Pearce-Higgins & Grant, 2006), although detailed studies are lacking.

To gain a mechanistic understanding of how livestock grazing pressure affects upland birds, replicated experiments that manipulate stocking densities are necessary, but rare. Experimentally managed sheep grazing in Norway resulted in a higher abundance of birds with increasing sheep density (Loe et al., 2007) while Johnson, Kennedy, and Etersson (2012) found that breeding success of two ground-nesting passerines in the United States did not vary with cattle grazing pressure. However, both studies investigated short-term bird responses in the first few years after the experiments had commenced. Land management change can take several decades, or longer, to reach their full effects on plant composition (Pakeman, Fielding, Everts, & Littlewood, 2019) and to have potential knock-on effects on other taxa across trophic levels. Yet to our knowledge, no experimentally managed grazing study has examined the long-term effects of grazing management on avian breeding success, largely due to the logistical and financial constraints of maintaining such experiments at large spatial scales.

Here, we use a replicated landscape-scale grazing experiment (the Glen Finglas experiment; Evans, Redpath, Evans, Elston, & Dennis, 2005) with 13 years of continuous manipulation to study the impacts of four livestock grazing treatments (i.e. sheep at two different stocking densities, mixed cattle and sheep grazing and no grazing) on meadow pipit *Anthus pratensis*, the most common passerine in the British uplands. Previous work using the Glen Finglas experiment has documented short-term effects on pipit breeding density (Evans et al., 2006, 2015) and egg size (Evans et al., 2005), which were both enhanced under low intensity, mixed cattle and sheep grazing. Furthermore, the pipit offspring sex ratio was

biased towards more male nestlings in plots with low-intensity sheep or mixed livestock grazing (Prior, Evans, Redpath, Thirgood, & Monaghan, 2011), while arthropod abundance and plant biomass increased with decreasing livestock densities (Dennis et al., 2008; Evans et al., 2015). However, there was no significant effect of grazing pressure on nest survival during the early years of the experiment (Evans, et al., 2005). Here, after more than a decade of continuous grazing, we predict that long-term effects of grazing management will have significant effects on nest survival and fledgling output, unlike results from early in the experiment. In particular, if meadow pipit breeding productivity is a function of vegetation structure and arthropod prey availability, we hypothesize that the effect of grazing pressure is enhanced in the later stage of the experiment, with lowest productivity in both the intensively grazed and ungrazed treatments. We investigate how grazing pressure and management duration affect the following measures of pipit breeding success: (a) breeding density, (b) clutch size, (c) hatch date, (d) number of fledglings per nest and estimated fledglings per plot and (e) egg, nestling and overall nest survival. Finally, although principally designed to understand the mechanisms by which grazing impacts pipit breeding productivity, we use the Glen Finglas experiment to investigate whether there are any long-term changes in the overall breeding bird community.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

A replicated, randomized block experiment, consisting of six replicates of four treatments, was initiated in 2003 at Glen Finglas, in central Scotland, United Kingdom (56°16'03"N, 4°25'08"W). The study site consists of largely wet and dry acid grassland with smaller areas of dwarf shrubs, bracken and willow scrub. Prior to the start of the experiment, the area was predominantly used for sheep grazing, with a density across the estate of approximately 0.7 ewes/ha, which declined during the course of the experiment. Meadow pipits are the most common breeding bird in the area and other bird species were uncommon in experiment plots when the treatments commenced. Each of the 24 experimental plots measures 3.3 ha. The plots were established over three spatial blocks, with random treatment allocation within each of six replicates (Figure S1). The blocks are situated approximately 5 km apart at an altitude of 200–500 m to cover variation in topography and soil type. The plot size was established to provide an anticipated sample size of 5 meadow pipit territories per plot, to yield sufficient statistical power when comparing the effects of treatment on breeding productivity. The grazing treatments were as follows: (I) *High*, commercial stocking density of sheep with nine ewes per plot (2.73 ewes/ha); (II) *Low*, one third of the commercial stocking density with three ewes per plot; (III) *Mixed*, two ewes per plot and, during 4 weeks each autumn, two cows with suckling calves and (IV) *Ungrazed*, without livestock. *Low* and *Mixed* treatments

were set up to both have low-intensity grazing pressures with the same annual vegetation biomass offtake and to maintain stocking at similar rates to those pre-experiment.

2.2 | Bird surveys, nest monitoring and vegetation sampling

The meadow pipit breeds in a range of grassland types and builds concealed nests on the ground. Incubation and nestling development each take approximately 13 days before chicks are ready to leave the nest. Breeding bird surveys were carried out in 2003–2004 and 2015–2016 to study immediate and long-term effects of livestock grazing treatments on meadow pipit breeding density and output. Breeding territories were determined by mapping all breeding activity of meadow pipit and other bird species during six surveys of each plot from late April to early July, with at least 3 days between each survey. Following Evans, Redpath, and Evans (2005), a territory was defined as a cluster with at least two independent observations of breeding behaviour (i.e. singing, alarming, food carrying or encounters of active nests) and territories could be separated from adjacent ones by simultaneous observations of singing males. Each year, territories were assigned to plots by the same method and person (DME) on maps of accumulated observations from surveys. On the small number of occasions when territories spanned two or more plots (9.9% of all territories), these were assigned to the plot where the majority of observations occurred. With standardized sampling effort, nests were located by searching through plots every 2–5 days, depending on weather conditions, through the whole breeding season. Nests were found by flushing incubating or brooding females while walking or rope dragging, and occasionally by observing birds arriving at the nests.

Once found, each nest was checked every 3 days (weather permitting) while active, through each stage of the nest period (i.e. egg laying to hatching and hatching to fledging, hereafter referred to as the egg and nestling stages). The meadow pipit lays one egg per day until a clutch of two to 5 eggs is completed. Partial predation was not observed in active nests, so the clutch size recorded when no additional eggs were found on following visits was therefore not likely to have been altered by predators. Partial mortality did occur (in 29% of nests), but unhatched eggs were then found in the nest and dead nestlings were found in or just outside the nest. A nestling was considered as successfully fledged when recorded alive just before fledging, unless it was found dead on the post-fledge visit on day 15–17 after hatching. The number of territories per plot was used as a measure for breeding density, but it was not possible to successfully find every nest within the plots. We therefore calculated the observed and estimated total number of fledglings per experiment plot. The observed number of fledglings per plot was the sum of all fledglings from all detected nests. To estimate the total number of fledglings per plot (i.e. when there were more territories than nests detected), we added a substitute number for each missing nest. This substitute number was calculated as the average number of fledglings per nest for the same treatment and year. As it is impossible

to know whether undetected nests were predated or just missed, we use both the number of observed and estimated fledglings in our analyses. The estimated number would be more accurate if all undetected nests were missed, and the observed number would be more accurate if all undetected nests were a result of predation.

To examine the influence of the initial vegetation community on pipit breeding output, vegetation was sampled prior to the set up of fences and experiment treatments in 2002. The vegetation communities were sampled by measuring cover of each plant species as the number of hits within a pin-frame at 25 locations per plot in late July to early August (Pakeman et al., 2019). We then measured vegetation height during each year of the bird surveys as the first hit of a sward stick at 50 points per plot between 10 May and 4 June. Although simplistic, this enabled testing of whether potential treatment effects on pipits are mediated through altered vegetation structure.

2.3 | Statistical analyses

All meadow pipit breeding parameters (see below) were analysed using GLMMs. Nests found after hatching were not used in proportional survival analyses for the incubation stage or total numbers of fledglings per nest. Within the models, treatment (categorical factor of the four grazing treatments) and sampling period (categories early or late) were the primary factors of interest, with the latter indicating either early (2003–2004) or late stage (2015–2016) effects of the treatments. A significant interaction between treatment and sampling period would indicate that grazing effects had changed between the two sampling periods. A significant effect of treatment across both sampling periods would suggest that any effect of different grazing pressure was already apparent at the early stage of the experiment. An effect of sampling period across all treatments would indicate that changes affecting the whole study area occurred between the two sampling periods, and therefore were unlikely to be related to grazing treatments.

The GLMMs for meadow pipit breeding density and the total number of breeding bird species per plot were tested with treatment and sampling period both as an interaction and as separate fixed effects. For meadow pipit breeding density, the number of territories of other bird species were also included as a fixed effect to control for potential disturbance/competition within the plots. The GLMM for Julian hatch date also contained grazing treatment and sampling period as an interaction and separate fixed effects, and the number of meadow pipit territories as a fixed numerical effect. The GLMMs for clutch size, number of fledglings, egg- and nestling-stage nest survival and overall survival all had the same fixed effects: treatment; sampling period; the interaction of treatment and sampling period; Julian hatch date; Julian hatch date² and number of meadow pipit territories per plot. The observed and estimated number of fledglings per plot were analysed similarly, but excluded the number of territories, which is directly linked to the estimate of fledglings per plot. Julian hatch date and Julian hatch date² (both numerical) were included to account for a linear and quadratic effect, respectively, of

seasonal variation. The number of territories was included to control for potential competition or positive effects by conspecifics. Fixed effects in all models were tested with likelihood ratio tests and removed sequentially if making the model worse in terms of model convergence and AIC score. All tests had the random effects: block (one of three experiment areas); replicate within block (which also takes into account altitude); plot; and calendar year, in line with Gelman and Hill (2006). Nest ID was also included in nest survival models as an observation level random effect (OLRE) to control for over-dispersion (Harrison, 2014). As the observed number of fledglings per plot may be affected by a potential difference between treatments in probability of finding nests, we first tested the effect of treatment on the ratio of nests found to territories per plot in a binomial GLMM. Details on selected models and probability distributions applied can be found in Table S2.

We further tested whether treatment effects on breeding productivity changed when taking initial vegetation communities into account, and whether potential effects of grazing treatment on productivity were mediated through a change in vegetation height. The models for breeding density and fledgling output per nest were therefore run with and without vegetation variables to determine whether the grazing treatment effects were affected by the initial vegetation communities and/or if they were solely due to vegetation changes. To characterize the initial vegetation communities in each plot, cover data from 2002 were subject to detrended correspondence analysis (DCA; Hill & Gauch, 1980) in CANOCO 5 (ter Braak & Smilauer, 2012; see Pakeman et al., 2019). Plot means for DCA axes 1 and 2, together with plot means for vegetation height, were used in separate models of breeding density and fledgling output with the same model structure as in the original models.

Since traditional r^2 values are not applicable to GLMMs we calculated marginal and conditional r^2 values, which provide estimates of variance explained by fixed effects only and by both fixed and mixed effects respectively (Nakagawa & Schielzeth, 2013). All models and graphs were analysed/produced in R version 3.5.2 (R Core Team, 2018). GLMMs were conducted using package `LME4` (Bates, Maechler, Bolker, & Walker, 2015). Post hoc tests for pairwise comparisons were carried out with package `LSMEANS` (Lenth, 2016) and p -values of the comparisons were adjusted with the Holm–Bonferroni method (Holm, 1979).

3 | RESULTS

Across the four breeding seasons, a total of 295 meadow pipit nests were found of which 268 were monitored until breeding outcome was confirmed (Table S1).

3.1 | Breeding density

The meadow pipit breeding density was significantly affected by grazing treatment across all years ($n = 96$, $\chi^2 = 15.59$, $p = 0.001$) with lowest

density in *Low* ($M \pm SD = 2.88 \pm 0.9$ territories/plot) and highest density in *High* (3.96 ± 1.37 territories/plot) and *Mixed* (3.92 ± 1.25 territories/plot). There was no interaction between grazing treatment and sampling period (Figure 1; Table 1) but there was a significantly higher breeding density in the early sampling period (3.81 ± 1.38 territories/plot) than the later one (3.27 ± 0.96 territories/plot; $\chi^2 = 4.09$, $p = 0.043$). Including

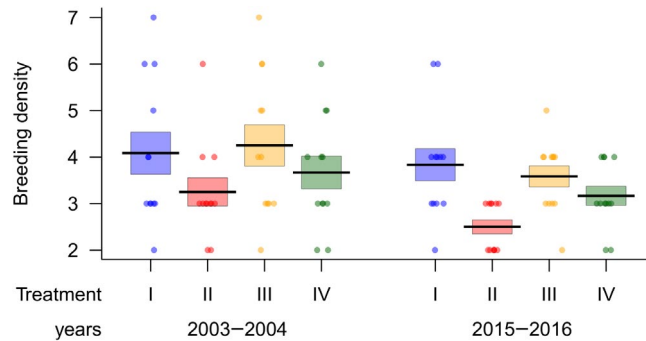


FIGURE 1 Breeding density of meadow pipits as territories per plot under four grazing treatments: (I) *High*, (II) *Low*, (III) *Mixed* and (IV) *Ungrazed*. Bars show means and boxes show standard errors. Raw data points are shown for each treatment and sampling period

TABLE 1 Results of GLMMs shown as χ^2 - and p -values and the explained variance by the model as Conditional r^2 . The interaction and independent effects of treatment and sampling period were tested in two separate models with the same final model structure. Treatment: factor with four grazing treatments—(I) *High*, (II) *Low*, (III) *Mixed* and (IV) *Ungrazed*. Sampling period: factor as either the early or late sampling period. Significant effects are marked in bold

Parameter		χ^2	p -value	Model Cond. r^2
Breeding density	Treatment × Sampling period	1.70	0.637	0.27
	Treatment	15.59	0.001	
	Sampling period	4.09	0.043	
Clutch size	Treatment × Sampling period	0.90	0.825	0.09
	Treatment	0.36	0.940	
	Sampling period	6.68	0.010	
Hatch date	Treatment × Sampling period	2.06	0.559	0.15
	Treatment	13.01	0.005	
	Sampling period	1.51	0.220	
No. of fledglings	Treatment × Sampling period	5.45	0.141	0.19
	Treatment	3.60	0.308	
	Sampling period	2.16	0.141	
Proportional nest survival:				
Eggs to fledging	Treatment × Sampling period	4.65	0.199	0.83
	Treatment	2.54	0.469	
	Sampling period	8.99	0.003	
Egg-stage	Treatment × Sampling period	6.70	0.082	0.85
	Treatment	10.07	0.018	
	Sampling period	16.52	<0.001	
Nestling-stage	Treatment × Sampling period	0.85	0.838	0.00
	Treatment	0.37	0.946	
	Sampling period	0.13	0.721	
No. of breeding bird species	Treatment × Sampling period	12.10	0.007	0.38
	Treatment	3.22	0.359	
	Sampling period	7.72	0.005	

vegetation variables in the model did not change the significance/non-significance of treatment and sampling period, but there was a significant effect of the initial vegetation community composition through the first DCA axis ($\chi^2 = 4.87$, $p = 0.027$; Table S2). Higher breeding density was associated with lower scores on the first DCA axis, plots with a higher abundance of mire species such as *Myrica gale* and *Narthecium ossifragum*. Higher scores on axis 1 where instead plots with a higher representation of acid grassland species such as *Agrotis capillaris* and *Anthoxanthum odoratum* (see Table S4; Figure S5 for all species).

3.2 | Clutch size and hatch date

There was no significant effect of grazing treatment or the interaction of grazing treatment and sampling period on clutch size (Table 1), but there were significantly fewer eggs laid per nest in the later sampling period (3.89 ± 0.6 eggs/nest) than the early period (4.1 ± 0.62 eggs/nest; $n = 239$, $\chi^2 = 6.68$, $p = 0.010$). Hatch date was affected by grazing treatment ($n = 239$, $\chi^2 = 13.01$, $p = 0.005$) with later hatching dates in *Low* than the other treatments (Julian date: *High* = 159 ± 17 , *Low* = 166 ± 18 , *Mixed* = 160 ± 17 , *Ungrazed* = 160 ± 18). However,

there were no significant changes in treatment effects between sampling periods (Figure 2; Table 1).

3.3 | Fledgling output and nest survival

The number of fledglings per nest was highest in *Low* and *Mixed* treatments but there were no statistically significant effects of grazing treatment across all years, nor by treatment–sampling period interaction ($n = 268$; Figure 3a; Table 1) or in the model including vegetation variables (Table S2). There was no significant effect of treatment on the probability of detecting nests (Table S5). There was also no significant effect of the interaction of treatment and sampling period or treatment alone on the estimated or observed number of fledglings per plot ($n = 96$; Figure 3b,c; Table S2).

Nest survival was highest in *Low* and *Mixed* treatments (Figure 4) but there was no significant difference in overall nest survival between grazing treatments or in the interaction of grazing treatment and sampling period. The proportion of eggs surviving until fledging was significantly higher in the early sampling period (survival: early = 0.61 ± 0.42 , late = 0.38 ± 0.42 ; $n = 240$, $\chi^2 = 8.99$, $p = 0.003$; Figure 4; Table 1). Egg-stage nest survival was significantly affected by grazing treatment ($n = 239$, $\chi^2 = 10.07$, $p = 0.018$) and sampling period ($\chi^2 = 16.66$, $p < 0.001$). The highest proportional egg survival was found in *Low* treatment (survival: *High* = 0.64 ± 0.43 , *Low* = 0.84 ± 0.30 , *Mixed* = 0.71 ± 0.40 , *Ungrazed* = 0.72 ± 0.40) and in the early sampling period (survival: early = 0.80 ± 0.34 , late = 0.60 ± 0.43); but there was no interaction of treatment and sampling period (Figure 4; Table 1). The nestling-stage nest survival was neither significantly affected by grazing treatment nor by the interaction of grazing treatment and sampling period ($n = 213$; Figure 4; Table 1). Of the nests considered for overall nest survival, 70 nests had partial survival during the incubation or nestling stage, while 87 nests failed completely and 83 had complete survival. Trampling was very rare (less than one nest per year on average). The majority (72%) of completely failed nests were a result of predation, which was higher in the later sampling period

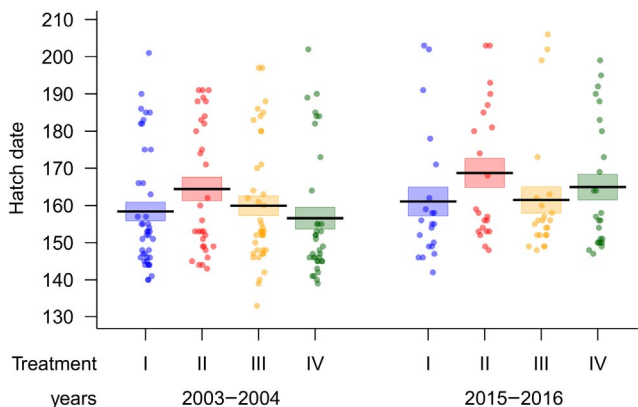


FIGURE 2 Julian hatch date for meadow pipit nests under four grazing treatments: (I) *High*, (II) *Low*, (III) *Mixed* and (IV) *Ungrazed*. Bars show means and boxes show standard errors. Raw data points are shown for each treatment and sampling period

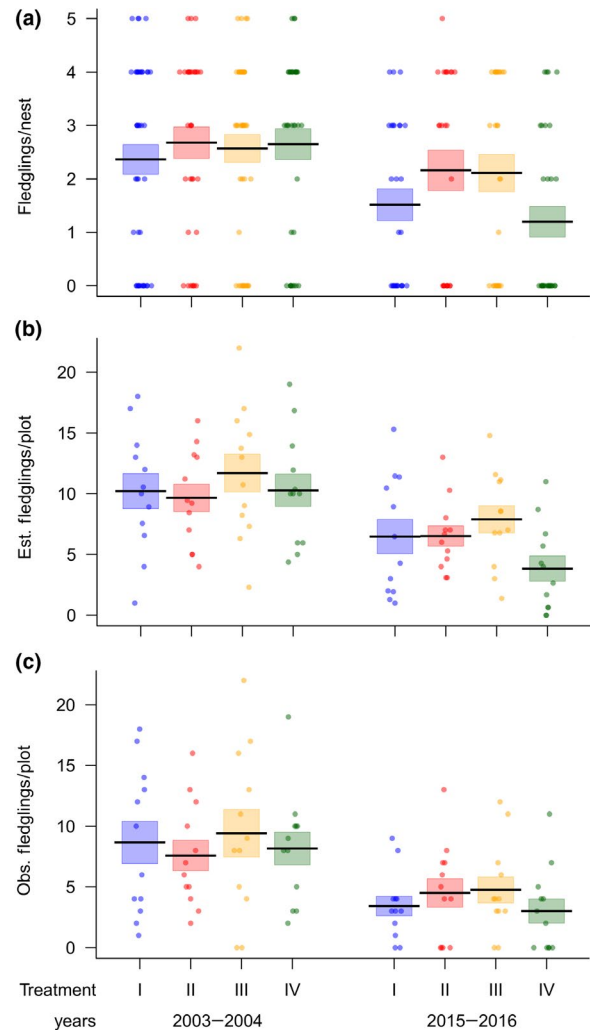


FIGURE 3 Number of meadow pipit fledglings (a) per nest, (b) estimated per plot and (c) observed per plot under four grazing treatments: (I) *High*, (II) *Low*, (III) *Mixed* and (IV) *Ungrazed*. Bars show means and boxes show standard errors. Raw data points are shown for each treatment and sampling period

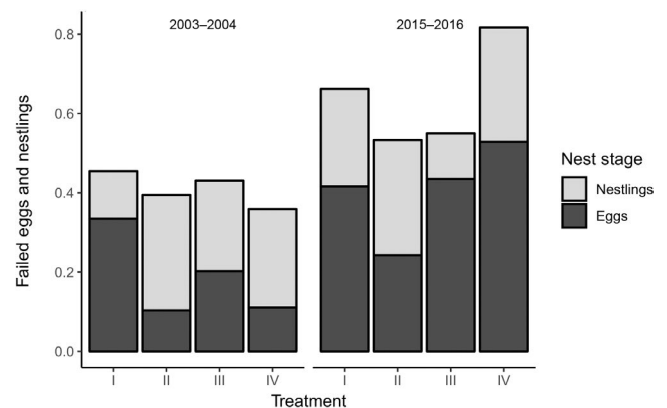


FIGURE 4 Proportional meadow pipit nest mortality for each treatment and sampling period during the period between egg laying and hatching (black bars) and hatching to fledging (grey bars). Full bars show average mortality proportions per nest for the whole period from egg laying until fledging. The grazing treatments were: (I) *High*, (II) *Low*, (III) *Mixed* and (IV) *Ungrazed*

(33%, compared to 17% in the early sampling period). Other nests were abandoned or did not hatch/died for unknown reasons.

3.4 | Breeding bird species richness

There was a significant interaction of treatment and sampling period on the number of bird species per plot ($n = 96, \chi^2 = 12.10, p < 0.007$). This

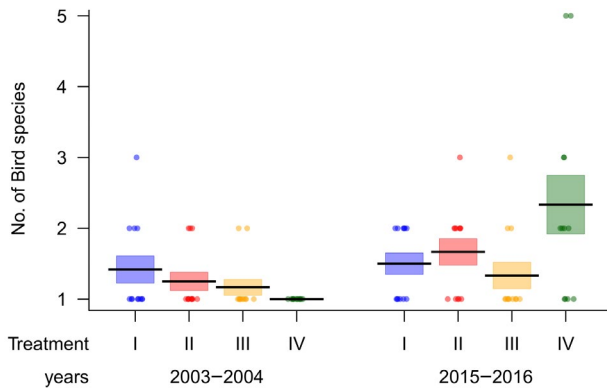


FIGURE 5 Number of bird species (including meadow pipits) holding breeding territories per plot. The four grazing treatments were: (I) High, (II) Low, (III) Mixed and (IV) Ungrazed. Bars show means and boxes show standard errors. Raw data points are shown for each treatment and sampling period

TABLE 2 Presence of breeding birds holding territories and/or observed nests. The figures indicate the sum of observed territories/nests if more than zero for all six replicates during the 2 years that make out each sampling period (early: 2003–2004, Late: 2015–2016). The four grazing treatments were: (I) High, (II) Low, (III) Mixed and (IV) Ungrazed

	Early sampling period				Late sampling period			
	I	II	III	IV	I	II	III	IV
Meadow pipit <i>Anthus pratensis</i>	49	39	51	44	46	30	43	38
Skylark <i>Alauda arvensis</i>	2	–	–	–	1	–	–	–
Grasshopper warbler <i>Locustella naevia</i>	–	–	–	–	–	–	–	1
Willow warbler <i>Phylloscopus trochilus</i>	–	–	–	–	–	1	–	4
Stonechat <i>Saxicola rubicola</i>	–	–	–	–	–	1	–	–
Whinchat <i>Saxicola rubetra</i>	–	1	–	–	–	2	2	5
Wheatear <i>Oenanthe oenanthe</i>	2	2	–	–	2	2	1	2
Reed bunting <i>Emberiza schoeniclus</i>	–	–	–	–	–	1	–	1
Black grouse <i>Tetrao tetrix</i>	–	–	–	–	–	1	–	3
Common cuckoo ^a <i>Cuculus canorus</i>	–	–	–	–	–	–	–	1
Mallard <i>Anas platyrhynchos</i>	–	–	–	–	–	–	–	1
Snipe <i>Gallinago gallinago</i>	2	–	4	–	3	–	1	–

^aCuckoo egg laid in meadow pipit nest.

was significantly higher in *Ungrazed* (2.33 ± 1.44 species/plot) than *Mixed* (1.33 ± 0.65 species/plot) in the later sampling period, while no significant differences between treatments were seen in the early sampling period (Figure 5; Table 1; Table S3). Seven bird species, including black grouse *Tetrao tetrix* and common cuckoo *Cuculus canorus*, were only observed breeding in the later period, and mainly in *Ungrazed* (Table 2).

4 | DISCUSSION

We provide the first experimental results of the long-term effects of livestock grazing intensity on the breeding performance of a common upland insectivorous passerine, as well as changes in the overall bird community. After a 12- to 13-year period, meadow pipit breeding density was significantly lower in the *Low* treatment. Conversely, the highest rates of egg-stage failure occurred in *High* and *Ungrazed* plots, where overall nest survival also tended to be lower, although not significantly so. There were no significant changes in grazing treatment effects over time but, across the experiment, both the egg-stage and overall nest survival declined with time. These results suggest that other processes at the wider landscape scale, such as changes in surrounding habitat and predator densities, are important for breeding meadow pipits and that these may be more apparent than long-term effects of variation in grazing treatment.

4.1 | Changes in treatment effects between sampling periods

Given the association of meadow pipits with habitat mosaics (Douglas et al., 2008; Pearce-Higgins & Grant, 2006), we hypothesized that positive effects of the low-intensity treatments (*Low* and *Mixed*) would be stronger on meadow pipit reproductive success in the later sampling period through changes in the vegetation structure and arthropod prey availability. Despite some intuitive trends, we found no statistically significant changes over time of grazing treatment effects on meadow pipit breeding parameters. Pakeman et al. (2019) showed that responses in vegetation community composition at Glen Finglas were slow in relation to the length of the experiment (see below) and inconsistent between vegetation communities. More productive acid grassland changed less than wetter mire communities (where the number of breeding pipit territories tended to be higher), even though all communities showed lower vegetation height in the *High* treatment. Furthermore, some of our models had a high proportion of unexplained variance (Tables 1; Table S2). Therefore, other factors such as weather and predation pressure unrelated to grazing treatments may contribute to a larger proportion of the variation in breeding success (see 'Long-term regional changes' below), but see Ibáñez-Álamo et al. (2015) for a summary of the possible interactive effects of food availability and increased predation risks.

Bird species richness in the experimental plots was affected by the duration of the grazing treatments, with highest species richness in the *Ungrazed* treatment in the later sampling period (Figure 5). Vegetation in the same experiment plots has been shown by Pakeman et al. (2019) to be tallest in the *Ungrazed* and *Low* plots, and shorter in *High* and *Mixed* plots, a difference that became more pronounced in the later stage of the experiment. Moreover, it took a minimum of 6, and sometimes 12 or 15 years for individual plant species to show a different response to grazing treatments (Pakeman et al., 2019). This suggests that changes in plant composition would not yet have been apparent in 2003–2004. Occasional additions of shrub species, that are able to settle or grow taller after the removal of grazing livestock, could potentially contribute to a more attractive habitat for a wider range of bird species (Calladine, Bielinski, & Shaw, 2013).

4.2 | Overall treatment effects

The highest meadow pipit breeding density was found in the *High* and *Mixed* treatments. This supports results from a landscape-scale sheep grazing study by Loe et al. (2007) in Norway, which found both meadow pipit and total bird abundances to be highest in intensively grazed plots compared to low intensity or ungrazed plots, at least in the short term. At Glen Finglas, the initial vegetation community composition, but not current vegetation height, had an effect on breeding density. Previous results from the early period of the experiment suggested that meadow pipit breeding

density is mainly driven by availability of arthropods that are common in upland bird diets (see Buchanan et al., 2006), where vegetation heterogeneity is high (Evans et al., 2015). Evans et al. (2015) also showed that vegetation height heterogeneity was greater in the *High* treatment while vegetation biomass and arthropod prey abundance were highest in *Ungrazed*, which suggests a trade-off between food abundance and food access in selecting breeding habitats. Although we were unable to simultaneously conduct detailed vegetation, arthropod and bird surveys each year, future work could examine potential treatment effects on the prey provisioned to nestlings.

The later hatching date observed in the *Low* treatment, although surprising, may be a result of less preferred habitat (also evidenced by lower breeding density in this treatment) and hence remaining available to individuals arriving late or perhaps being in poorer condition. This could be confirmed by further territory mapping aimed at comparing changes in breeding density throughout the season and assessing the condition of caught adults. However, there was no treatment effect on the observed or estimated fledgling output per plot. Instead, *Low* plots had the highest egg-stage nest survival, which could suggest a mismatch in site preference versus suitability. It can be harder for arriving birds to predict predation risks compared to food availability when selecting breeding territory (Misenhelter & Rotenberry, 2000). At Glen Finglas, previous studies found that activity indices of foxes *Vulpes vulpes* were highest in *Ungrazed* plots and declined as a result of increasing grazing pressure (Villar, Lambin, Evans, Pakeman, & Redpath, 2013). The higher nest failure rate in *High* plots could instead be explained by an increased exposure to predators through lower vegetation biomass (Baines, 1990), or even by predation by sheep (Jarrett et al., 2017).

4.3 | Long-term regional changes

Several breeding parameters were affected by sampling period across all grazing treatments with smaller clutch sizes, lower overall nest survival, (near significantly) fewer fledglings per nest and lower egg-stage nest survival in the later sampling period (Table 1). Considering that most nests failed due to predation, the change in nest survival is likely caused by a regional change in predation pressure, and meadow pipit breeding success (but not local breeding density) has been observed to increase under experimental predator removal (Fletcher, Aebischer, Baines, Foster, & Hoodless, 2010). The area of native woodland on the estate on which this study is located has increased during the course of the experiment. This could contribute to the higher nest predation in the later period by providing increased cover for predators (Söderström, Pärt, & Rydén, 1998), but more research is necessary. The growing interest in natural woodlands, afforestation and rewilding will drive the need to find ways for such management to work effectively in parallel with traditional land use such as grazing (Pettorelli et al., 2018).

5 | CONCLUSIONS

Our results show that longer term effects of grazing intensity can affect the breeding density and egg-stage nest survival of the meadow pipit, with lowest survival in *High* or *Ungrazed* plots, but that over 12–13 years this has little effect on overall nest survival or number of fledglings produced. Treatment effects on fledgling output were not significantly stronger in the later period of the experiment. Instead, there was lower nest survival in the late compared to early sampling period, mainly caused by predation across all grazing treatments. Grazing exclusion was associated with an increase in bird species richness in the later stage of the experiment, probably due to a gradual change in vegetation structure and composition. Further studies disentangling the effects of regional predator abundances and local management on both predator numbers and predator behaviour would be needed to identify the causes of observed predation pressure on breeding birds.

ACKNOWLEDGEMENTS

This project was funded by the Macaulay Development Trust, Newcastle University, University of Hull, and the British Trust for Ornithology, UK. A.J.K. and R.J.P. were supported by the Strategic Research Programme funded by the Scottish Government's Rural and Environment Science and Analytical Services Division. We thank Woodland Trust Scotland for permission to use and access the Glen Finglas Estate and especially thank the shepherds who managed livestock in the plots. We also thank Aifionn Evans, Anja Kunaver and Debbie Fielding who contributed to collecting the data. The long-term experiment is administered by the James Hutton Institute.







AUTHORS' CONTRIBUTIONS

D.M.E., J.W.P.-H., L.E.M., N.A.L., A.J.K., S.M.R. and R.J.P. designed and/or managed the experiment; L.E.M., D.M.E., E.K., R.J. and N.A.L. collected the data; L.E.M. analysed the data and wrote the first draft. All the authors contributed substantially in shaping the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.9zw3r22bd> (Malm et al., 2020).

ORCID

Lisa E. Malm  <https://orcid.org/0000-0002-7412-9515>
 James W. Pearce-Higgins  <https://orcid.org/0000-0003-1341-5080>
 Nick A. Littlewood  <https://orcid.org/0000-0003-4461-8833>
 Alison J. Karley  <https://orcid.org/0000-0002-0252-2086>
 Robin J. Pakeman  <https://orcid.org/0000-0001-6248-4133>
 Stephen M. Redpath  <https://orcid.org/0000-0001-5399-9477>
 Darren M. Evans  <https://orcid.org/0000-0003-4061-6726>

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How to cite this article: Malm LE, Pearce-Higgins JW, Littlewood NA, et al. Livestock grazing impacts components of the breeding productivity of a common upland insectivorous passerine: Results from a long-term experiment. *J Appl Ecol*. 2020;00:1–10. <https://doi.org/10.1111/1365-2664.13647>