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Does sward density affect prey availability for grassland birds?

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Abstract

Measurements of the effects of sward height, density and heterogeneity (usually % bare soil) are often confounded in field studies of bird habitat preferences and their effects are difficult to disentangle. This study experimentally investigated how changes in sward density alone affected the foraging behaviour of starlings *Sturnus vulgaris* L., small passerines that feed on soil invertebrates in grassland. High- (24,000 tillers m^{-2}) and low-density (12,000 tillers m^{-2}) ryegrass *Lolium perenne* L. swards, created using a combination of cutting and fertilization treatments, were grown under greenhouse conditions. These density treatments were representative of sward densities in extensively and intensively managed fields in the wider countryside. Trios of starlings were placed in individual enclosures on top of these turfs, which covered trays containing a sand base topped with randomly located invertebrate prey (mealworms). Starlings foraged successfully on both dense and sparse sward treatments. No differences in foraging behaviour, intake rates or intake efficiency were attributable to sward density.

Keywords: Sward structure; Grassland; Foraging behaviour; Bird declines; Agriculture; Starlings

1. Introduction

Since World War II, lowland grassland management has changed through the increased use of inorganic inputs, drainage of damp grassland and increases in stocking density. Grass swards have lost their diversity and have became dominated by a small number of fast-growing, palatable species, many of which required ploughing and reseeding every few years (Shrubb, 2003; Tallowin et al., 2005). These changes have implications for the structure and composition of the sward and the abundance and accessibility of food resources within it (Atkinson et al., 2005; Wilson et al., 2005).

Cropping patterns have also changed in modern pastoral farming. Grazing pressures have increased with stocking densities (Fuller and Gough, 1999), and 85% of cut grassland production is now silage and 15% is hay, compared to almost all in hay production 60 years ago. Grass cut for hay must dry sufficiently before storage (>88% dry matter for leafy swards, 82–85% dry matter for mature swards) (Merry et al., 2000). Hay can be made from dense swards but because of the unpredictable climate hay swards tend to be more open and sparse and are cut later when the crop is mature to expedite drying. Grass produced for silage can be grown in denser, more productive swards because it can be baled with a higher moisture content (20–60% dry matter) (Merry et al., 2000). Lowland grassland swards are characterised by dense, fast growing ryegrass *Lolium* spp. cultivars (see Tallowin et al., 2005; Vickery et al., 2001). These are managed under high inputs of inorganic nitrogen fertilizer to increase yields, and rolling to prevent soil contaminating the product. In addition, hay is normally cut once in June or July when periods of warm, dry weather are more likely, whereas silage is usually cut from early May

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and as regularly as every 6 weeks through until September/October.

One of the by-products of either intensive cutting or grazing is an increase in sward density (Garay et al., 1999; Lawson et al., 1997). Defoliation promotes the production of tillers (shoots) because light penetrates through to the base of the plant and stimulates vegetative growth, and short cropping also promotes a prostrate growth habit (Garay et al., 1999). Both factors cause a high tiller density in regularly cut or grazed swards (e.g., Fisher et al., 1995; Orr et al., 1990). Even in the absence of changes in invertebrate abundance, changes in sward density may affect the foraging behaviour and success of birds. Dense swards may present a greater level of obstruction to the soil below and reduce prey accessibility (Wilson et al., 2005).

The understanding of how different aspects of sward structure, such as height, density and heterogeneity (usually % bare soil or tussockiness of the sward), contribute to bird habitat preferences is often confounded by the interaction of these variables. Individual features are often difficult to disentangle and may be confounded with unmeasured features, such as prey distribution and abundance, when studied in the field. This study uses an experimental approach to disentangle the effects of sward density from other sward features, and uses standardised prey abundance and distribution. The effects of swards density on the foraging behaviour of a typical grassland insectivore, the European starling *Sturnus vulgaris* L., were investigated by comparing the bird's behaviour when foraging on dense and sparse swards (representative of swards grown under intensive and extensive management systems). If tiller density affected foraging behaviour, intake should be lower on denser swards. Starlings are one of the farmland bird species that are Red-listed in the United Kingdom because their population numbers have declined by more that 50% during the past 25 years (Gregory et al., 2002, 2004). Starlings preferentially forage in permanent pastures and consume grassland invertebrates (Whitehead et al., 1995), primarily leatherjackets (commonly *Tipula paludosa* Meigan larvae) living in the top few centimetres of the soil.

2. Methods

This study took place at the John Krebs Field Station, Wytham, Oxfordshire, between January and March 2003. Thirty-six starlings from the local population were captured under English Nature licence using whoosh nets and were colour-ringed for identification. They were housed indoors, in groups of three, in 0.9 m × 0.7 m × 0.6 m cages until all trials were completed, after which they were released from the capture site (mean time in captivity = 36 days, maximum = 63 days). Starlings were aged and sexed using a combination of morphological traits including iris colour, spot size and shape and throat feather length, which is accurate in 98% of cases (Smith et al., 2005). Thirty of the 36 starlings were randomly selected to be focal birds (10/11 adult males, 9/12 1st winter males, 2/4 adult females, 9/9 1st winter females). They were maintained under a light:dark cycle that reflected prevailing conditions and each cage was in visual and auditory contact with other groups. Starlings received a diet of ad libitum turkey starter crumb and softbill pellets, and a 2.5 cm^3 daily ration of mealworms was provided after trials were completed. Water for drinking and bathing was available at all times.

A silage long-term ley mix of ryegrass *Lolium perenne* L. cultivars was grown using a hydroponic (soil-less) system in a glasshouse to create the sward. During August 2002, seed was sown at a rate of 50 g m^{-2} onto a bed (1 cm depth) of medium-grade vermiculite, an inert, sterile growing medium. The inert medium was chosen over soil to prevent contamination with invertebrate eggs or larvae that could damage the sward and provide cues about a prey's location for a foraging bird, and to produce a uniform sward.

The beds were housed on 2 m × 4 m raised tables overlaid with a perforated polyethylene tarpaulin. Beds received an initial fertilizer treatment of soluble Phostrogen, a broad-scale fertilizer containing nitrogen, potassium and phosphorus plus essential trace elements. It was applied in liquid form using a hose-end adapter at the manufacturer's suggested rate. Beds were watered as necessary throughout the experiment. Once seeds germinated approximately 10 days after sowing, beds were allocated to one of two sward density treatments: sparse and dense. Dense beds continued to receive Phostrogen fertilizer three times every week, whereas sparse beds were fertilized once every other week. Dense beds were cut to a height of 3 cm twice a week from November onwards to promote tillering. Sparse beds were not cut. To stimulate continued vegetative growth the glasshouse was heated from October to March to maintain the temperature above 5 °C overnight and 15 °C during the day. During the same time period the beds received additional sulphur lighting from 6 a.m. until 8 p.m. daily.

A 1 cm thick root mat around the growing medium was produced by both sward treatments. This allowed the sward to be cut into 0.5 m × 0.5 m squares and lifted as a turf. On the day of testing turfs were cut to 3 cm height and clippings were removed. Swards were cut to this height for two reasons. Firstly, starlings preferentially forage on short grass in farmland (Bamett et al., 2004; Tucker, 1992; Whitehead et al., 1995), where their foraging effort is greater (Devereux et al., 2004). Secondly, sward density declines with increased height, because shading from the sward canopy prevents light from reaching the stem bases, which is required to stimulate vegetative growth. Other than changes in density, no other differences were detected between dense and sparse swards. No invertebrates were discovered in either treatment.

Three enclosure set-ups were placed in a linear arrangement in a glasshouse with a gap of 0.35 m between cages. The glasshouse had whitewashed sides to prevent visual disturbance from outside. Each enclosure set-up consisted of a 0.5 m × 0.5 m plastic tray (35 mm deep) filled to a depth of 25 mm with wet fine sand. Twenty-five circular cells measuring 60 mm in diameter and 25 mm tall were inserted into the sand in each tray in five rows of five. The combination of wet sand and cells were used to restrict prey (mealworm) movements. Ten cells in each tray were randomly selected to contain prey and five live mealworms were placed into each (50 per tray equating to a density of 200 prey m^{-2}). A density of 200 prey m^{-2} (two million - ha^{-1}) is within the upper end of the range of observed densities of leatherjackets in pasture fields (Blackshaw and Coll, 1999; Blackshaw and Newbold, 1987). A higher prey density was chosen because tipulid-feeding birds typically select fields with the greatest biomass of prey in which to forage (Whitehead et al., 1995), and two million prey ha^{-1} is typical of selected fields (e.g., Pearce-Higgins and Yalden, 2004). Mealworms were grouped to represent a clumped distribution as occurs with leatherjackets in pasture meadows. A 0.5 m × 0.5 m turf cut to 3 cm was placed on top of the sand and a bottomless enclosure was placed on top of the turf. The enclosures were constructed of lightweight wire mesh and were cubic with side length 0.5 m. A Sony Hi8 digital camcorder on a tripod was placed 2 m in front of the central cage and was used to video record the trials.

Each of the 30 focal birds experienced one replicate of each density treatment leading to 60 trials being performed. Each focal individual also served as a companion to two others. The 30 birds therefore experienced six trials in total, two as a focal individual and four as a companion. Trial order number was the sequence number (1–6) when each individual was recorded as a focal bird, which was randomly assigned. Each focal bird's companions were randomly selected from the remaining stock. If the same two companions were selected for more than one focal bird, a new draw was performed to ensure that all of the 30 experimental trios were different to avoid possible pseudoreplication. The same companion pair were present for both of the focal bird's trials to ensure that the focal bird's foraging rate was not influenced by individual differences in its companion's rates, because foraging rates are mediated by the rates of other flock members (Fernández-Juricic and Kacelnik, 2004).

No bird, whether acting as a focal or a companion, received more than one trial in a day. On average each bird was used in the experiment once every 4 days (number of rest days between trials ranged from 1 to 11 days). Individuals were transported to the glasshouse in soft cotton bags. One companion bird was released into each end enclosure and the focal bird was placed in the central enclosure. The observer retreated from the glasshouse and the trio was left to forage. If birds did not forage during the first 10 min after release the trial was abandoned. Trials lasted 15 min from the first probe (noted by the experimenter through a spy hole in the glasshouse door) after which birds were returned to their cages.

2.1. Data collection

Videoed trials were converted to digital media files and randomly assigned a code. Behavioural data were extracted 'double-blind' from media files using the Noldus Observer event recorder by an assistant. All behavioural variables are described in Table 1. We distinguished between time spent foraging and time spent performing other behaviours. A foraging bout was initiated with a head-down (head below the body's horizontal plane) and terminated by a head-up (head above the body's horizontal plane) lasting longer than 5.6 s (the median value obtained from a previous study (Devereux, unpublished data)) and included all behaviours in between such as short scans. The total time spent foraging was the sum of all foraging bouts within the 15 min trial. Two states with measured duration (head-up, head-down) and three instantaneous events (probe, root, eat) were recorded. Probe and root were both prey searching behaviours occurring during head downs. Probe was classified as the initial bill stab that caused a hole in the turf, and a root was a further stab within the hole that functioned to expand it and extract prey. The following behavioural response variables were computed from videos (Table 1): total time spent foraging, mean duration of a searching bout (sec), search rate (number of head downs performed per sec foraging), mean duration of a scan (head up), scan rate (number of head ups per sec foraging), probe rate (probes per sec foraging), root rate (roots per sec foraging), intake rate (prey per sec foraging), and intake efficiency (prey per 100 roots).

2.2. Data analysis

Factor analysis was used on the starling's behavioural responses using the principal component extraction method

Table 1
Description of the foraging and vigilance variables used in this study

Variable	Description
Head down	Head lowered below body's horizontal plane
Head up	Head raised above body's horizontal plane
Probe	Initial stab into soil
Root	Secondary stabs into soil in location of probe hole
Foraging bout	Duration between the start of a head-down and the start of a head up l asting longer than 5.6 s
Total time spent foraging	Sum of foraging bouts
Mean search duration	Mean length of head down
Search rate	Number of head downs/total time spent foraging
Mean scan duration	Mean length of head up
Scan rate	Number of head ups/total time spent foraging
Probe rate	Number of probes/total time spent foraging
Root rate	Number of roots/total time spent foraging
Intake rate	Number of prey captured/total time spent foraging
Intake efficiency	Number of prey captured/100 roots

to reduce the multi-dimensionality of our dataset (eigenvalues > 1). The resulting factors are composite and uncorrelated variables that summarise the variation in foraging behaviour seen. All response variables except intake efficiency were used, in order to avoid including two similar measurements (intake rate and intake efficiency). The scores from principal component analysis were used as the response variables in Repeated Measures GLMs (all analyses were conducted in SPSS for Windows v 13.0.1, SPSS Inc., Illinois). Models were constructed with sward density as our within-subject factor and sex and age as between-subjects factor. The same Repeated Measures GLMs were also performed on the response variables intake rate, intake efficiency and total time spent foraging to further validate our results. Trial order number (1–6) was not correlated with any of the response variables and therefore was not included in analyses (Spearman's R, $P > 0.15$ in all cases). When a between-subject factor had neither a significant main effect nor interaction with density, it was removed and analyses were re-run. Probabilities quoted are two-tailed.

3. Results

The combination of fertilizer treatment and cutting regime was successful in producing swards of two distinct densities. At the time of testing dense swards had approximately 24,000 tillers m^{-2} and sparse swards had approximately 12,000 tillers m^{-2}. As sward density appeared consistent both between and within grass beds, and because the foraging activity of starlings damaged the cut mats, tiller density in individual mats was not measured on a trial-by-trial basis. The densities used reflected naturally occurring densities in multi-cut silage meadows/heavily grazed pastures and traditional hay meadows respectively (Fisher et al., 1995; Orr et al., 1990).

Three of the starlings did not forage in one of their trials (two on sparse treatments, one on dense treatment) and the remainder foraged in an apparently normal manner in both treatments. Birds located and captured between 0 and 35 of the 50 mealworms per 15 min trial (mean ± S.E. captures overall: 5.93 ± 0.47; dense swards: 5.94 ± 0.69; sparse swards: 5.93 ± 0.69).

After factor analysis, two factors were identified which had eigenvalues >1. The third factor had an eigenvalue of 0.98 and represented the one variable that neither of the first two factors did so adequately. Three factors were therefore chosen for principal component analysis, which represented 76.8% of the cumulative variance in foraging behaviour. PCA 1, which explained 43.4% of the variance, represents the contrasting effect of search and scan rates, with search and scan length (Table 2). High PC1 scores represented a strategy of frequent switching between scanning and short searches, with high probe rates. PCA 2, which explained a further 23.1% of the variance, represents the contrasting effect of search length and root rate. High PC2 scores represented increased bout length but a low rooting intensity (Table 2). PCA 3, which explained 12.2% of the variance, represents the duration of time devoted to foraging during a trial (Table 2). High PC3 scores represented a longer total foraging duration. There were no significant interactions between sward density and the between-subject factors, age and sex in any of the analyses performed. Therefore, results quoted exclude these factors (note: there was no difference in the significance of any of the results if the between subject factors were included or excluded).

Table 2
Loadings of the eight foraging and vigilance variables on the first three PCA axes

Variable	PCA1	PCA2	PCA3
Total time spent foraging	−0.203	−0.322	0.782
Mean search duration	−0.139	0.636	−0.003
Search rate	0.449	−0.269	0.204
Mean scan duration	−0.474	−0.096	−0.012
Scan rate	0.509	0.000	−0.192
Probe rate	0.394	0.164	0.119
Root rate	0.117	−0.524	−0.245
Intake rate	−0.290	−0.329	−0.486

Sward density had no effect on any of the principal component score foraging variables: PC1: $F_{1,26} = 1.844$, $P = 0.19$; PC2: $F_{1,26} = 0.44$, $P = 0.51$; PC3: $F_{1,26} = 0.198$, $P = 0.66$. Sward density also had no effect on any of the raw foraging variables (Table 1 for description): intake rate: $F_{1,26} = 1.049$, $P = 0.32$; intake efficiency: $F_{1,26} = 2.041$, $P = 0.17$; total time spent foraging $F_{1,26} = 1.152$, $P = 0.29$.

4. Discussion

Sward density had no detectable effect on the foraging and vigilance behaviour of starlings. In this study the distribution and density of prey were kept constant between treatments. Thus, these results demonstrate that sward density within the range of 12,000–24,000 tillers m^{-2}, representative of extensive and intensive managed pastures and meadows, did not affect starling foraging behaviour and the accessibility of prey. This is in agreement with some field studies which have shown that sward density itself is not a good predictor of field use by insectivorous passerines (Bamett et al., 2004; Perkins et al., 2000). Other studies have shown negative effects of density on habitat use across a wide range of agricultural swards. For example, yellow wagtails *Motacilla flava flavissima* L. establish territories on grass swards that are short, sparse and contain more patches of bare soil (Bradbury and Bradter, 2004). However, most of the field studies confound sward height and density characteristics and refer to the avoidance of tall, rather than short, dense swards, or confound density with heterogeneity (bare soil measures, e.g., Moorcroft et al., 2002).

In a previous study, with a similar design and sample size, starlings captured more prey when foraging on short grass compared with long grass (Devereux et al., 2004). Thus, the lack of a density treatment effect is likely to be because its biological significance as tested here is too small. One of the benefits of foraging on short swards is that birds can monitor the environment for predators simultaneously whilst feeding, allowing them to capture more prey over the same time period (Devereux et al., 2006; Whittingham and Evans, 2004). Short swards may also improve access by reducing the physical obstructions to locating and removing prey, and may improve mobility (Wilson et al., 2005). It seems that for starlings, which forage by probing the soil for hidden invertebrates, the key variable to foraging success is sward height rather than density.

Prey abundance, in addition to prey accessibility, may be affected by management practices which produce swards of differing densities. In farmed environments, high sward densities are associated with frequent cutting or grazing (Tallowin et al., 1995), because defoliation is the trigger that stimulates vegetative growth. Both mowing and grazing can increase short-term foraging success through increases in foraging efficiency or prey availability (Devereux et al., 2006b; Morris and Thompson, 1998).

The longer-term effects of short dense swards on invertebrate abundance are poorly understood. It is likely that short dense swards will contain fewer invertebrates for three reasons. Firstly, surface and foliar invertebrate biomass may be reduced because of limited opportunities for foraging and shelter (Morris, 2000). Secondly, dense, fast-growing swards will have higher evapotranspiration rates (Garwood, 1988) resulting in drier soils that are less easy to probe for access to soil invertebrates. Finally, short dense swards may harbour fewer prey, because they are drier (Maccarone, 1987), structurally and climatically homogeneous (Vickery et al., 2001), and because a dense sward reduces soil surface temperature, which all lead to a decrease in the number and diversity of invertebrates (Wakeham-Dawson and Smith, 2000). Overall, although starling foraging success was unaffected by sward density per se, dense, agricultural swards may be less productive habitats for foraging birds through a combination of effects on prey abundance, size and accessibility.

Although starling foraging success was unaffected by sward density, the same may not be true for birds that locate prey on the soil surface by sight, such as thrushes, because a dense canopy may reduce prey detectability to a greater extent. The level of canopy cover and thus, physical obstruction, may not be a simple reflection of sward density. Several studies have highlighted the importance of bare ground for ground foraging birds, such as granivores, thrushes, wagtails and pipits (Atkinson et al., 2005; Moorcroft et al., 2002; Perkins et al., 2000). Areas of bare soil may provide small birds with opportunities to forage at the soil surface when canopy cover is dense. This is unlikely to be true for starlings in grassland systems as bare ground will have few tipulids, which feed on the roots and stems of grass below the surface. Managing grassland in a way that provides foraging opportunities for a range of bird species will almost certainly require a heterogenous mix of tall and short swards and patches of bare ground to provide habitat for the invertebrate prey (often in tall swards) and habitat where these prey are accessible to birds (short swards or bare ground) (Atkinson et al., 2005; McCracken and Tallowin, 2004).

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