The effect of sward height and drainage on Common Starlings *Sturnus vulgaris* and Northern Lapwings *Vanellus vanellus* foraging in grassland habitats

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Agricultural change is often cited as a causal factor in the decline of the UK’s farmland birds because bird declines have mirrored changes in agricultural practices. Although much is known about the mechanisms driving population declines on arable systems, mechanisms in grassland systems are relatively poorly studied, despite receiving a similar degree of intensification. Agricultural intensification may affect bird declines by reducing food abundance or accessibility, forager mobility or predation risk. Here we examine experimentally the effects of sward height on the foraging behaviour of adult Common Starlings *Sturnus vulgaris*, and the effects of sward height and drainage on the behaviour of Northern Lapwing *Vanellus vanellus* chicks. Both species are declining across the UK and both forage in farmed grassland habitats, but they differ in their foraging methods because Starlings probe for soil invertebrates whereas Lapwing chicks glean prey from surfaces. Overall, after controlling for prey abundance, short swards were found to be more productive for both species. Prey capture rate within foraging bouts did not differ with sward height for Starlings, but Starlings spent more time foraging on short swards and captured 33.2% more prey. Starlings walked more steps on short swards. Lapwing chick foraging rates declined as sward height increased. Soil moisture was not found to be a predictor of Lapwing chick foraging rates within the observed range. Our results suggest that short swards are a more profitable foraging habitat for soil and surface invertebrate feeders. Short swards may facilitate surface prey detection, improve forager mobility and increase foraging time by altering vigilance patterns. Provision of short swards in areas where these are lacking could be simple method of improving foraging habitats for grassland birds.

Agricultural landscapes predominate the UK, covering more than three-quarters of its land area (Defra 2003 statistics, available at http://www.defra.gov.uk) and many bird species are now associated wholly or partially with agricultural land. There is widespread evidence that during the past four decades a high proportion of birds associated with farmland have declined in abundance or contracted in range (Marchant & Gregory 1994, Tucker & Heath 1994, Fuller et al. 1995, Siriwardena et al. 1998, Krebs et al. 1999, Gregory et al. 2002, Newton 2004). During recent years research on arable farming systems has improved our understanding of the mechanisms driving changes in biodiversity (Aebischer et al. 2000). Grassland habitats, which have also gone through a period of intensification as arable land, have received relatively little attention in this respect, despite covering two-thirds of the UK’s agricultural land (Fuller 1987, Wakeham-Dawson & Smith 2000, Vickery et al. 2001).

Since the Second World War the UK’s grasslands have declined in area and been agriculturally improved to increase productivity (Shrubb 2003). Permanent pastures have been converted to arable land to meet increased cereal requirements. Within arable systems temporary grass leys have been replaced by other

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crops such as oilseed rape, reducing farm-scale heterogeneity with the result that the east has become predominantly arable and the west pastoral (Robinson & Sutherland 2002, Benton et al. 2003). Grassland systems have been improved to utilize marginal habitats and to increase production and profitability (Stoate 1996). Wet grasslands have been drained and traditional pastures, meadows and rough grazing have been fertilized and reseeded with competitive species, which often require ploughing and reseeding every 5–10 years. This change in management has allowed an increase in stocking density and a switch from hay to silage production (Stoate 1996, Wakeham-Dawson & Smith 2000).

Changes in grassland management are thought to affect bird populations through prey abundance and availability, predation risk and forager mobility (Vickery et al. 2001, Benton et al. 2002, Atkinson et al. 2004, Buckingham et al. 2004, Whittingham & Evans 2004). Intake rates of foraging birds will depend upon habitat structure (Whittingham & Markland 2002), and it seems plausible to expect that changes in grassland management may have affected prey availability. For example, fertilization increases sward growth and density, which could increase mobility costs and predation risk and decrease prey availability.

Both Northern Lapwing Vanellus vanellus and Common Starlings Sturnus vulgaris are declining across the UK (Gregory et al. 2002). It has been suggested that recent changes in grassland management have contributed to the decline in grassland birds by reducing food abundance and by creating habitats that are unsuitable for foraging (Galbraith 1988a, Milsom et al. 2002). Although both Lapwing broods and Starlings often forage in short vegetation within grasslands, the mechanisms behind this association are unknown (Perkins et al. 2000, Milsom et al. 2002). Here we report the findings of two experiments investigating the effects of grassland management on the foraging success of Lapwings and Starlings, grassland birds that forage on surface and soil invertebrates, respectively (Feare 1984, Baines 1990, Beintema et al. 1991). Studying the foraging success of birds is preferred to direct measurements of food abundance as a method of assessing habitat suitability because it reflects the resources available to foragers (Whitehead et al. 1996). In experiment 1 we examined the effects of sward height and soil moisture on Lapwing chick foraging behaviour and success and in experiment 2 we examined the effects of sward height on Starling foraging behaviour and mobility.

We predicted that food intake in short swards would be greater because prey are easier to detect and capture and swards are easier to move through. Food intake should increase with soil moisture because invertebrate density is thought to be greater in damp (but not flooded) habitats (Milsom et al. 2002).

**METHODS**

**Lapwing chicks**

This study was carried out on the Gruinart Flats part of the RSPB Loch Gruinart Nature Reserve on the Isle of Islay. Gruinart Flats comprises six fields (86.1 ha in total) of agriculturally improved and semi-improved grassland with a traditional rig and ditch structure. The Flats are managed for wintering geese and breeding Corncrake Crex crex, Spotted Crake Porzana porzana and waders, including Lapwing (175–200 pairs) and Redshank Tringa totanus (50–100 pairs). The hydrology of the Flats is controlled by a system of sluiced canals along field boundaries and a series of shallow ditches that run along the length of each field. Water control of individual rigs is achieved by attaching 90° angled pipes on individual outflow drains, which allows or restricts water flow out of rigs. Fertilizer is applied to the Flats to promote grass growth for Corncrake cover, silage for winter feed, to maintain the mineral balance of the soil and achieve successful reseeds. A 15 : 8 : 15 nitrogen–phosphorus–potassium blend is applied to rigs at the rate of 750 kg/ha each year.

This experiment was designed to investigate the effects of sward height and soil moisture on Lapwing chick foraging behaviour and success. During 2002 the timing of fertilizer application and level of water in ditches had been manipulated at a field scale at Gruinart Flats as part of a wider experiment investigating the effects of grassland management on Lapwing food supply and breeding ecology (McKeever 2003). This resulted in a range of soil moisture levels and sward heights available for Lapwing broods to forage on. Fifteen colour-ringed Lapwing chicks aged 5–10 days from ten broods were located and observed foraging on one occasion at Gruinart Flats between 4 and 16 May 2002 between 07:00 and 11:00 hours. Observations were not made in adverse weather such as rain and windy conditions when chicks were brooded by adult females. Observations were made using a Kowa TSN telescope with a ×30 magnification wide-angled lens and 8 × 42 magnification binoculars from a Landrover used as a mobile...
Sward height and drainage effects on foraging

Chicks were observed between 20 and 30 m from the landrover and chicks were equally visible in all sward heights measured (1–10 cm). Observation sessions lasted between 1 and 2 h (mean 1.2 h).

Chicks alternated between foraging bouts that were initiated with a peck, and being brooded by adult birds or performing other behaviours such as preening. Foraging rates were recorded in the form of ‘peck rates’ and ‘successful peck rates’. Pecks were defined as attempts to catch food whether successful or not. Successful pecks were defined as observed food intake. Foraging bouts were timed and overall numbers of pecks and successful pecks in that time were recorded. After foraging bouts, ten sward height and ten soil moisture measurements were collected at random from where chicks were observed feeding. The location where chicks fed was recorded as ditch if chicks were within 1.5 m of the ditch centre, and rig when chicks fed on the 10-m-wide raised rigs between ditches. Chick foraging rates (overall and successful) were then calculated and analysed in relation to mean sward height, soil moisture and rig or ditch location.

Starlings

We conducted this study between January and March 2002 at University Farm, Wytham, Oxfordshire. Locally captured Starlings were colour-ringed and housed in groups of two and three in 0.9-m × 0.7-m × 0.6-m indoor cages under a light–dark cycle that reflected local conditions. They received a diet of turkey starter crumb, Orlux pellets and mealworms and were fed daily after trials were completed. Water was available ad libitum. Starlings were released once the experiment had finished.

We used four bottomless 0.5-m³ wire mesh cubic enclosures placed onto intensively managed permanent pasture that was mown to either 3 cm (short) or 13 cm (long), to represent a heavily grazed or mown sward and a sward without winter grazing or mowing, respectively. Short and long swards were mown at the same time 4–7 days prior to being used, to control for a possible temporary flush response in foliar invertebrate prey. One sward height treatment was randomly allocated to each of eight patches in a field to control for natural variation in leatherjacket prey abundance. Although leatherjackets can redistribute when conditions are unfavourable (D. McCracken pers. comm.) it is unlikely that mowing to the heights used would cause significant changes in their abundance. Cages were arranged in a square within patches with two levels of neighbour distance as part of a larger study into the effects of flock density on foraging behaviour.

Twenty Starlings were selected as focal individuals for testing and each had three companions during trials. During testing one bird was released into each enclosure and the behaviour of the focal individual was recorded using a digital video camera placed 3 m from the cage. A trial lasted for 15 min after probing for prey commenced, which was usually within 1 or 2 min. One trial was abandoned because the focal bird did not forage within 10 min of entering the cage. Each focal bird received one replicate of each treatment and no more than one trial in a day. Presentation order was randomized and the study area was covered between trials to prevent depredation by wild birds.

Starlings alternated between periods of active foraging and other behaviours such as vigilance and preening. We defined an active foraging bout as a foraging event initiated when the head was lowered below the horizontal plane of the body and terminated when the head was raised above this plane for more than 5.6 s (the median length of this behaviour and a break considered long enough to represent the natural end of a foraging bout). Analysis and results are restricted to active foraging bouts. We coded videotapes using Noldus Observer Video Pro 4 (Noldus Information Technology 1997) and recorded the number and type of prey captured, the frequency of probes (initial substrate investigations) and roots (subsequent substrate investigations within the location) and the number of steps walked.

Data analysis

Data were analysed using general linear models (GLM, normally distributed data) and general linear mixed models (GLMM, Poisson distribution and logarithm link function), automatically controlling for overdispersion (R. Payne, pers. comm.). Brood (Lapwings) or individual (Starlings) was entered into models as a random effect to control for repeated measures of subjects or broods. Minimal models were arrived at by backward selection and GLM residuals were checked for normality. The significance of covariates or treatments as predictors of foraging behaviour or success were assessed in GLMM by the Wald statistic under a χ² distribution. Predicted fits were used to display results controlling for other terms remaining in the model.
RESULTS

Lapwing chicks

Successful peck rates were found to be significantly related to overall peck rates \( (R^2 = 0.797, F_{1,35} = 137.9, P < 0.001) \), implying that food intake is directly dependent on factors determining the overall peck rate of Lapwing chicks. As ‘overall’ and ‘successful’ peck were correlated, the effects of sward height and soil moisture were only investigated on overall peck rates.

Overall peck rates varied significantly with sward height and location within the field. Foraging rates in fields declined significantly as sward height increased \( (\chi^2 = 20.38, P < 0.001; \text{Fig. 1}) \). Surface invertebrate abundance, measured using pitfall traps, did not vary significantly between long and short swards (McKeever 2003), suggesting that sward height was restricting Lapwing chick intake rate, probably through reducing chick mobility or food availability (accessibility). The same trend was observed when foraging rates between rigs and ditches were analysed. Foraging rates in ditches, which have shorter swards (McKeever 2003), were significantly greater than on rigs \( (\chi^2 = 14.58, P = 0.002; \text{Fig. 2}) \). However, food abundance was significantly greater in ditches than on rigs (McKeever 2003). Soil moisture was not found to be a predictor of foraging rates when sward height and rig/ditch location were controlled for \( (\chi^2 = 0.04, P = 0.84) \). However, spring 2001 was a particularly wet season and our inability to detect an effect of soil moisture may reflect the range of moistures we observed (range 5.1–5.4 m\(^{-3}\)): our drier soils could have been sufficiently damp for foraging requirements.

Starlings

Starlings spent 29.9% more time actively foraging on short swards \( (254.1 \pm 25.8 \text{ s}) \) than on long swards \( (195.6 \pm 17.1 \text{ s}) \) during the 15-min trial \( (F_{1,78} = 7.64, P = 0.008) \). Few non-leatherjacket prey were captured and so prey types were combined for analysis (205 leatherjacket vs. ten other prey during 80 trials). Starlings captured 33.2% more prey on short swards than on long swards \( (\chi^2 = 5.02, P = 0.03; \text{Fig. 3}) \). This reflected the time devoted to foraging on each height treatment, because there was no change in intake rate (captures per second of active foraging) between sward heights (captures per second: \( F_{1,78} = 1.43, P = 0.24 \)). Starlings foraging in short swards walked more steps than those foraging in long swards \( (F_{1,78} = 11.7, P = 0.001) \).

Figure 1. The effect of sward height on overall peck rates per min of Lapwing chicks. Peck rate declined significantly as sward height increased \( (\chi^2 = 20.38, P < 0.001) \). Each data point represents the predicted foraging rate for a given sward height from the model.

Figure 2. Comparison of Lapwing chick predicted overall peck rates between rigs and ditches, controlling for other factors and covariates. Error bars represent one standard error around each mean. Peck rates were significantly greater on ditches than on rigs \( (\chi^2 = 14.58, P = 0.002) \).

Figure 3. The effect of sward height on the predicted number of prey consumed by Starlings, controlling for other factors and interactions. Error bars represent one standard error around each mean. Starlings consumed significantly more prey when foraging on short swards than when foraging on long swards \( (\chi^2 = 5.02, P = 0.03) \).
DISCUSSION

Several key results emerge from these two studies with respect to the effect of sward structure of foraging behaviour of Starling adults and Lapwing chicks. Overall, short swards were more productive for both species studied. Lapwing chick foraging rates were greater on grass than on swards because prey abundance was greater and swards were shorter (McKeever 2003). Variation in foraging rates between swards is therefore likely to be a direct consequence of increased food abundance and availability. As water levels in ditches retreat over the season, areas of bare soil become available, providing unrestricted access to an abundant food supply. Within swards or ditches Lapwing chick foraging rates declined as sward height increased, even though there were no differences in food abundance. Again, when prey were equally abundant in short and long swards, Starlings spent more time foraging on short swards and captured 33.2% more prey over time. Starling movement was greater in short swards. Soil moisture was not found to be a predictor of Lapwing chick foraging rates within the range studied.

When selecting fields in which to forage, birds face choices in the trade-offs between food abundance, food accessibility and predation risk (Butler & Gillings 2004, Whittingham & Evans 2004). A recent field study investigating the effects of grassland management intensity on birds and their food resources discovered a surprising lack of evidence between food abundance and field usage (Fuller et al. 2003, Atkinson et al. 2004). They did find strong relationships between short swards and field preference in many species and concluded that factors other than food abundance can drive foraging choices. Our results suggest that even in the absence of differences in prey abundance, habitat structure can determine food intake rates for both adult Starlings and Lapwing chicks. There are a number of factors that may account for this relationship, including foraging surface area, different prey assemblages between habitats, prey availability (accessibility), mobility and vigilance rates. Recently, studies on the foraging success of Canaries Serinus canarius have demonstrated a negative relationship between food detection and habitat structural complexity because more complex environments present a greater surface area over which to forage (Whittingham & Markland 2002). The increased surface area of tall grass swards could explain why foraging rates of Lapwing chicks, which feed on surface invertebrate prey, declined.

Starlings, which forage predominantly on Tipulid prey hidden beneath the soil surface, captured more prey on short swards. In our study we found no difference in Starlings’ foraging rate within foraging bouts, suggesting that prey availability was not driving the relationship. However, Starlings spent less time foraging on long swards, and consequently more time with their head raised when not foraging. Starlings are social foragers and monitor the environment for predators and the behaviour of their congeners for foraging or scrounging opportunities. They have wide (Type 1) visual fields (Fernandez-Juricic 2004), and recent research has shown that such species can react to predators while foraging in a head-down position (Lima & Bednekoff 1999). In obstructed environments, such as the tall grass sward treatment of our experiments, these monitoring opportunities can only occur while the head is raised, forcing a change in vigilance patterns and an associated reduction in foraging time (Metcalfe 1984). Therefore, differences in monitoring opportunities with habitat structure could drive the foraging patterns of Starlings by altering their vigilance behaviour.

Another hypothesis that our data support is the role of habitat structure in mobility. Starlings walked more steps on short swards, corroborating an earlier study that showed movement rates of Starlings were greater on lawns that were mown short (Brownsmith 1977). Unfortunately, Lapwing chick movements were not measured in our study, but they have relatively short legs and are not well adapted to long vegetation (Galbraith 1988b). It is probable that food intake can be compromised by restricted mobility.

Regardless of the mechanism driving the relationship between foraging success and sward height, fine-scale management of habitat structure could be a useful conservation tool for grassland birds. In common with many other species of birds that breed and forage on farmland, Starling and Lapwing populations are declining in the UK (Gregory et al. 2002) and across much of northern Europe (Schifferli 2000, Donald et al. 2001). During the period of the decline, Starling breeding performance per nesting attempt has shown a slight but significant improvement whereas the number of broods per season does not appear to have changed (Feare & Forrester 2002, Siriwardena & Crick 2002). Survival of first-year birds and adults, however, has fallen, probably because of a reduction in food or habitat availability (Crick et al. 2002, Freeman et al. 2002). Lapwings declined rapidly in lowland Britain through the
1980s, probably because of changes in agricultural practices that have led to a decline in Lapwing productivity (Hudson et al. 1994, Wilson et al. 2001, Baille et al. 2002).

Many studies have demonstrated habitat associations of farmland birds, including some showing preferences for short swards (Whitehead et al. 1995, Perkins et al. 2000, Fuller et al. 2003), but few have been able to identify which factors are important (see Chamberlain et al. 1999). This study allowed us to isolate and evaluate the importance of sward height and drainage from other confounding factors, such as prey abundance, that are often present in broad-scale habitat associations. For example, we were able to disentangle the relationship between soil moisture and sward height by showing that soil moisture did not affect intake rates within the range of soil moisture occurring in our study site (McKeever 2003). However, our study area was wetter than many other parts of the UK and relationships between soil moisture and foraging rates have been demonstrated elsewhere for Lapwings and waders (Milsom et al. 2002).

Our results, that short swards improve foraging rates by increasing food accessibility and reducing predation risk and mobility costs, are applicable to other species foraging in similar habitats. For example, wintering flocks of Fieldfares Turdus pilaris and Redwing Turdus iliacus often forage in mixed flocks in pasture alongside Starlings, and also feed on soil-and surface-dwelling invertebrates. The amber-listed Meadow Pipit Anthus pratensis hunts visually for surface-dwelling insects in a similar manner to Lapwing chicks. Redshank and Curlew Numenius arquata breed and feed on agricultural grasslands. Even species feeding on seeds and other food types, such as Turtle Doves Streptopelia turtur and Yellowhammers Emberiza citrinella, may benefit from improved food accessibility and predator detection that short swards offer.

Habitat suitability could be improved for Starlings, Lapwings and other grassland invertebrate feeders by maintaining areas of short sward where short swards are lacking by grazing or mowing. Intensive sheep grazing produces apparently desirable short swards, but increases in sheep numbers have accompanied declines in Starling and Lapwing populations during recent decades (Fuller & Gough 1999). At the same time, cattle numbers have remained constant (Vickery et al. 2001). Cattle and sheep grazing have different effects on sward structure (Vickery et al. 2001, McCracken & Tallowin 2004). Intensive grazing by sheep reduces sward structural complexity and promotes short bowling-green-type pastures. Moderate grazing, especially by cattle, increases structural heterogeneity and leads to patchy swards with areas of long and short cover. Although sheep grazing in particular may benefit prey accessibility, its effects on prey abundance are not well understood.

The interaction between sward height and invertebrate prey abundance is complex. Although short grass swards may be beneficial for finding food and monitoring the environment, over time they may have lower prey densities because they offer fewer resources and less protection for soil and surface invertebrates (Jones & Jones 1984, McCracken et al. 1995). Managing grassland habitats for breeding Lapwing also requires the provision of longer sward to provide adequate cover for nesting adults and chicks from predators (McKeever 2003). A solution may be a spatial and temporal mosaic of sward heights in pastures and meadows, maintained by selective grazing and mowing at different times of the year (McCracken & Tallowin 2004). Patches of long sward would provide protective cover from predators and reservoirs of invertebrate prey, and short swards would give foragers unobstructed environments and access to these prey. Thus, small-scale heterogeneity in sward height would offer kitchens and dining rooms for foraging grassland birds. Loss of habitat heterogeneity at all scales has been suggested as a key determinant in loss of farmland biodiversity, and loss of sward heterogeneity may explain the inverse relationship observed between sheep densities and Starling and Lapwing populations (Benton et al. 2003).

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