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Mid-season shifts in the habitat associations of Yellow Wagtails *Motacilla flava* breeding in arable farmland

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Declines in habitat quality through the breeding season within a bird's home-range can limit overall productivity. In environments where multiple breeding opportunities arise during the course of a season, these effects can be buffered by a shift to different breeding sites or habitats. We studied the distribution and habitat associations of a crop-nesting farmland bird, the Yellow Wagtail *Motacilla flava*, across an arable-dominated farming region in eastern England using both field-scale territory mapping and large-scale transect surveys. Surveys were repeated at monthly intervals to measure changes in both distribution and habitat use during the course of the season. The distribution of breeding birds changed markedly at both regional and field-scales, coinciding with a shift in crop preference. Initially, most territorial birds were recorded in autumn-sown cereal fields, but this crop was subsequently abandoned in favour of potato crops, which were more patchily distributed. Other habitat features influencing Yellow Wagtail distribution included local crop diversity, hedgerow presence and soil type, with organic soils supporting higher abundance than alluvial clays or silts. The mid-season switch in habitat associations might allow individuals to maximize the number of breeding attempts made in a single year by using multiple habitats sequentially. The use of multiple habitats could influence population regulation by buffering the effects of local within-season declines in habitat suitability. Seasonal habitat switching may be more prevalent than is currently recognized in seasonal environments.

Keywords: agriculture, breeding dispersal, nesting attempts, plasticity, territory abandonment.

In many bird species, reproductive success is influenced not only by the number and quality of offspring produced during a single breeding attempt, but also by the number of breeding attempts made within a single season (Newton 1998, Powell *et al.* 1999). Several factors can limit the number of breeding attempts made, including energetic constraints of reproduction and rearing of young (Tinbergen & Dietz 1994, Ogden & Stutchbury 1996), and exogenous constraints such as breeding season length (Wilson *et al.* 1997). Resource depletion, or other factors such as temporal changes in habitat structure, can lead to short-term declines in habitat quality within an established home-range (Jackson *et al.* 1989, Soderstrom 2001). In such circumstances, breeding activity may be curtailed unless alternative sites or habitats can be used. In agricultural landscapes of fast-growing crops, seasonal variation in habitat structure is often apparent and can strongly influence habitat suitability for farmland bird species (Brickle & Harper 2002, Browne & Aebischer 2003, Newton 2004). For multi-brooded species, the exploitation of several consecutive breeding habitats or sites within a season might allow individuals to maximize breeding

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productivity within seasonally variable environments such as farmland. Despite the recent proliferation of research on farmland bird ecology, this phenomenon has been examined in few species.

Life-history strategies involving shifts in breeding habitat or distribution during the course of a single season are poorly documented. In most birds, dispersal predominantly occurs during non-breeding periods, either between years or, most often, during a post-juvenile exploratory phase prior to the first breeding attempt (i.e. natal dispersal, Greenwood & Harvey 1982, Paradis *et al.* 1998). Mid-season breeding dispersal has been documented in several species of cardueline finches, with shifts in breeding ranges occurring in response to consecutive peaks in seed-food availability in different forest types (Antikaenen *et al.* 1980, Newton 2000). Mid-season breeding dispersal has also been documented in Quail *Coturnix coturnix* (Aebischer & Potts 1994), Grey Wagtail *Motacilla cinerea* (Klemp 2003), Sedge Wren *Cistothorus platensis* (Bedell 1986), Black-throated Blue Warbler *Dendroica caerulescens* (Betts *et al.* 2008), Prairie Warbler *D. discolor* (Jackson *et al.* 1989) and Red-billed Quelea *Quelea quelea* (Jaeger *et al.* 1986). However, most species are thought to exhibit strong site fidelity during the breeding season (Greenwood & Harvey 1982). Indeed, habitat association studies frequently assume that breeding distributions remain static once initial settlement has occurred at the start of the breeding season (Betts *et al.* 2008).

In agricultural landscapes, habitat features such as vegetation height, density and appearance can change dramatically during the course of a year. In two ecologically similar multi-brooded crop-nesting passerines, the Yellow Wagtail *Motacilla flava* and the Skylark *Alauda arvensis*, habitat suitability in arable farmland is known to change over the course of the season in relation to patterns of crop growth. In both species, early breeding attempts frequently occur in autumn-sown cereal fields, but subsequent changes in crop height and sward density mean that these fields become unfavourable for later breeding attempts (Stiebel 1997, Wilson *et al.* 1997, Donald *et al.* 2002, Eraud & Boutin 2002). If suitable habitats are available elsewhere, an adaptive strategy in response to such changes might be to abandon the initial territory and perform mid-season breeding dispersal. In the case of the Skylark, late broods are known to occur in other habitats such as root crops and set-aside (Wilson *et al.* 1997, Donald *et al.* 2002); Skylarks holding territories in areas that lack late-season breeding habitats are generally thought simply to cease breeding activity after the initial attempt (Jenny 1990, Eraud & Boutin 2002). Given the predominance of autumn-sown cereal cropping within European agriculture (Stoate *et al.* 2001), this early curtailment of breeding activity is thought to be a significant driver of population declines in this species (Donald *et al.* 2002). In the case of the Yellow Wagtail, studies in Germany have suggested that seasonal changes in the distribution of breeding pairs may occur, with preferences shifting from winter cereals in the early season to spring-sown crops such as sugar beet and potatoes at later stages (Stiebel 1997). In the UK, the habitat requirements and site tenacity of Yellow Wagtails within arable farmland have been little studied (Wilson & Vickery 2005), and little is known of the influence of within-season changes in habitat favourability on the distribution of breeding activity.

Quantifying patterns of dispersal on a meaningful scale using traditional mark–recapture methods is notoriously difficult in wild populations (Betts *et al.* 2008). In this study, we use a large-scale repeated transect method to monitor the distribution of breeding Yellow Wagtails across an arable landscape during a single breeding season. This method allows us to examine seasonal changes in territory distribution and habitat use at a population scale. We also use intensive territory mapping and nest searches within smaller study sites to examine seasonal changes in breeding distribution at the field scale. Using these two approaches, we aim to assess whether changes in habitat selection occur during the course of a single season, and whether such changes cause shifts in Yellow Wagtail breeding distribution across our study area. We consider the role of habitat association plasticity for individual and population productivity within this environment, and identify key habitat requirements for this declining species, populations of which have fallen by 65% in the UK since 1972, fulfilling criteria for red-listing as a species of high UK conservation priority (Vickery *et al.* 2004, Eaton *et al.* 2006).

METHODS

Large-scale survey

Study area and site selection

A total of 190 transect sites were surveyed across an extensive tract of agricultural land in the counties of Lincolnshire, Cambridgeshire, Norfolk and Suffolk, UK (*c.* 5000 km^2, Fig. 1). This region, collectively known as the East Anglian Fens, forms a basin drained by three heavily canalized rivers: the Nene, the Welland and the Great Ouse. The region is extremely flat, ranging from −2 m to 8 m asl. Data from the Land Cover Map 2000 (http://www.ceh.ac.uk/sci-programmes/BioGeoChem/LandCoverMap2000.html) show that agriculture is the dominant land use within this area; approximately 61% of the land falls under arable cropping and 21% under grassland. The region is characterized by an open aspect, with large fields (mean of fields surveyed 16.9 ha ± 9.4 sd) and a lack of trees and hedges relative to most lowland agricultural landscapes in the UK. Most field boundaries consist of drainage ditches, grass strips, roads or tracks.

Using 1 : 25 000 maps, we identified all potentially accessible linear transect routes of 1 km within the region, excluding urban or wooded areas. These included single-lane roads, tracks, public byways and public footpaths, as well as routes on private land organized through existing access agreements. Given the open aspect and linear nature of most access routes within the study region, we were able to identify 450 potential linear transects (ensuring that no individual site was within 3 km of another to minimize the likelihood of spatial autocorrelation). From this pool of potential transects, 190 were randomly selected. Three visits were made to each transect, spaced 1 month apart, between May and early August 2004. Visits were made between 08:00 and 17:00 h during periods of clear weather with winds below 20 km/h. Periods of highest song activity (i.e. early morning) were avoided to limit the potential for bias resulting from diurnal variation in detection rate. All data collection was carried out by four experienced observers.

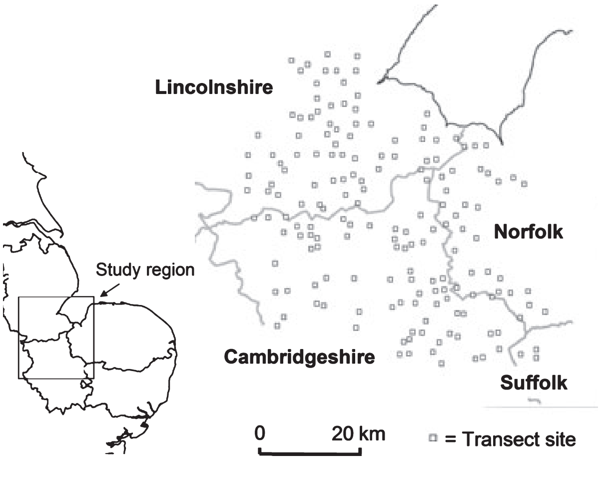

Figure 1. Map of Fenland study region in eastern England, showing locations of 1-km transects, county boundaries and North Sea coastline.

Territory recording

On each monthly visit, the full transect was walked slowly by one observer, stopping at 100-m intervals to make 360-degree scans with binoculars. Transects were walked at a uniform pace, such that each was surveyed in a period of 30–40 min. The location of each Yellow Wagtail encountered was recorded on a sketch map showing all fields and field boundaries. Yellow Wagtails do not defend a strict feeding territory and will forage up to 1.5 km from the nest-site (Smith 1950, Roselaar 1988). Various behaviours are, however, characteristically displayed around nest-sites or advertisement territories. These include singing, song flights and aggressive behaviour by males, which tend to be displayed both prior to nest establishment and during chick rearing (Roselaar 1988). Food provisioning, carrying of nesting material or faecal sacs, and mobbing or alarm calling are also indicative of breeding activity. When a nest is present, alarm calling usually begins at distances of around 200 m from the observer (J. J. Gilroy, pers. obs.). Birds showing any of the above behaviours were taken to indicate territory presence. Each record was assigned to the field over which the behaviour occurred. Where possible, birds in direct flight were followed until landing, and their subsequent activity class was recorded. Adult birds engaged in other activities (e.g. feeding) were not included in territory classification, but were recorded to estimate relative variation in the total number of individuals across sites. However, juvenile birds were excluded from all datasets as their distribution may not reflect breeding habitat selection. In cases where a male and female were recorded performing territorial behaviours in close proximity, only a single territory was classified. For each sighting, the distance from the observer was estimated, in addition to the angle of deviation from the main transect line, allowing calculation of perpendicular distances from the transect (Buckland *et al.* 2001). These data were used to estimate the effective sampling area from transects and to explore the effects of habitat and time of day on bird detection.

Habitat variables

Descriptions of all the habitat variables recorded, and the scale at which they were measured, are listed in Table 1. Habitat data were recorded for all fields directly adjacent to the transect line. Fields were defined as blocks of similar cropping, meaning that adjacent areas of the same crop with different sowing dates (i.e. different heights) but lacking any other separating boundary feature, were still classed as separate fields. Field dimensions were calculated using 1 : 25 000 maps in MapInfo V6.5 GIS software (Pitney Bowes Ltd, Windsor, UK). In cases where field boundaries were not marked on maps, visual estimates of boundary position were used. Habitat data were also recorded for all field boundaries of each field surveyed, including those directly adjacent to the transect line. For each boundary encountered, an estimate was made of the area occupied by each feature as a proportion of the whole field boundary, the size of which was determined from field dimensions. Additional habitat information was taken from maps, including the number of buildings and woodlands within 500 m of each transect, as well as soil type, identified using a 1 : 100 000 soil map (Soil Survey of England and Wales, 1983). For ease of interpretation, similar soil classes were lumped into broad categories following Avery (1980), as shown in Table 1. When transects ran across a soil-type boundary, the soil was classified as the type underlying the majority of the transect line.

Field-scale survey

Study area

To assess field-scale habitat selection, we carried out intensive territory mapping and nest searches during 2005 across six areas of exclusively arable farmland in Lincolnshire and Cambridgeshire, covering 33 km^2 across 14 different farms (see Gilroy *et al.* 2008 for a detailed description of these sites). All farms were intensively managed, with all surveyed fields receiving broad-spectrum herbicide, fungicide and fertilizer treatments during the study period. Cropped land occupied a minimum of 80% of the total area on each site. All sites were dominated by autumn-sown cereal cultivation (38% of total area surveyed), with other principal crops being field beans (13%), oilseed rape (12%), peas (10%), sugar beet (8%) and potatoes (5%). Soils on intensive study sites varied both within and between sites, covering a broad spectrum from peat-rich soil to heavy clay-rich soil, creating a locally patchy mosaic of soil conditions.

Table 1. Habitat variables recorded at each transect. Variables with 'field' as the unit of measurement were summed to give a single figure for each transect in analyses.

Variable	Unit of measurement	Description
Crop type	Field	Identified where possible
Crop height	Field	Visually estimated within 20-cm height bands
Field dimensions	Field	Measured from 1 : 25 000 maps when boundaries were marked, otherwise visually estimated
Bare areas	Field	Area estimated for patches exceeding 5 m^2
Boundaries	Field	
Grass margin		Length and width estimated
Ditch		Length, width of open water and presence of emergent vegetation
Bare ground		Length and width estimated
Hedge		Length and height estimated
Track/road		Length and width estimated and substrate recorded
Buildings	Transect	Total number encountered within about 500 m of transect
Woodland	Transect	Area estimated or taken from map for patches over 20 m^2
Soil types	Transect	Taken from Soil Survey of England and Wales, Sheet 4 (1983), combining the following standard soil categories from Avery (1980):
Loam		Cat. 5.1, 5.3, 5.6
Peat		Cat. 8.5, 8.7, 10.2
Sand		Cat. 5.5, 8.2
Silt		Cat. 3.7, 8.12, 8.3
Clay		Cat. 8.11, 8.13
Elevation	Transect	From Ordnance Survey 1 : 25 000 maps
Cropping diversity	Transect	Simpson's R index for whole transect

Territory mapping and nest monitoring

Each study site was comprehensively surveyed twice a month during the 2005 breeding season (April–August) using territory mapping methodology (Marchant 1983). Census routes followed field boundaries or tramlines within crops, such that all areas of each field were visited to within 50 m. Sightings and activities of Yellow Wagtails were recorded using the same behavioural classification scheme as the large-scale survey described above. Every care was taken to avoid double-counting of individuals during each survey. Once areas of potential breeding activity were identified, nests were located either by observation of adults returning to the nest-site or by systematic searches of the area of focal activity. Nests were found at various stages of the breeding cycle, including nest building, incubation and chick provisioning. Nests were visited at 3-day intervals, recording clutch or brood size on each visit. Nests from which the clutch or brood disappeared before fledging (i.e. < 12 days after hatching) were assumed to have been predated. The date of failure (or fledging) was estimated as the mid-point between the last visit when the nest was active, and the date on which the outcome was known.

Statistical analysis

Large-scale habitat associations

To identify habitat factors influencing Yellow Wagtail distribution across the large-scale transect survey area, models were constructed using each 1-km transect as a sample unit. Territory count across each transects was modelled as the response variable. Areas of each habitat type were summed for each transect, giving a single value for each factor. Field sizes were truncated following appraisal of distance–detection curves, such that only areas within the maximum range of Yellow Wagtail detection (delimited as the zone including 95% of detections) were considered (in this case up to 300 m from the transect route). Field boundary variables were also constrained to within this detection zone. Separate models were generated for each monthly survey (May, June and July, with some visits from early August included in the July dataset).

Data were gathered for a large number of habitat variables considered to have the potential to influence the distribution of Yellow Wagtails (Table 1). To maximize the information gained, a two-stage analysis was performed. Initially, hierarchical partitioning was used to explore the independent influence of all measured factors on Yellow Wagtail distribution. This method reduces the possibility of assigning false importance to variables as a result of multi-collinearity in the dataset, as well as allowing simultaneous comparison of a large number of candidate variables (MacNally 2000). Once factors with an independent influence on Yellow Wagtail distribution were identified, information theoretic approaches were used to determine the combination of these variables that best predicted variation in the response variable (Anderson *et al.* 2000).

The hierarchical partitioning process was performed using the R statistical package (http://www.r-project.org/). The hierarchical partitioning protocol fits a series of generalized linear models with a Poisson error distribution and log link function. The randomized method of transect selection removed any need for the inclusion of a spatial random effect. All possible combinations of the candidate variables were modelled, although quadratic and interaction terms were not considered due to sample-size limitations and the large number of candidate models required. Log-likelihood ratios were used to measure the change in goodness of fit upon addition of each variable to each model combination. These measures were then averaged over all combinations in which a given variable was included, using the HIER.PART package (Walsh & Mac Nally 2008). This provides a measure of the independent effect I of that variable, which is robust to collinearity with other variables in the set. The statistical significance of the independent effect was tested by randomization (MacNally 2000). Data were randomized 1000 times, giving 1000 different values of I for each variable. The observed value was then tested against the randomized distribution via the Z score:

$$Z = ([\text{observed} - \text{mean}\{\text{randomizations}\}]/\text{SD}\{\text{randomizations}\})$$

with statistical significance based on the upper 95% confidence limit.

Once a subset of significant predictor variables had been identified using hierarchical partitioning, information theoretic approaches were used to determine the combination of variables that best predicted the data and to generate robust estimates of parameter coefficients. Model selection was performed using Akaike's Information Criterion (AIC), calculated for generalized linear mixed (GLM) models with Poisson error and log link function and fitted using the R statistical package. All possible combinations of variables were ranked according to their AIC score (lower is better), and Akaike weights (AIC_w) were calculated to demonstrate the relative probability that each candidate model best predicts variation in the response variable (Burnham & Anderson 2002). As the number of candidate models increases exponentially with the number of model terms included, interactions between predictor variables could not feasibly be considered. In cases where no single candidate model was clearly superior to other models (i.e. difference in AIC between the two best models < 6), we calculated model-averaged parameter estimates and unconditional standard errors. Parameter selection probabilities were generated by summing the Akaike weights of all models including a particular parameter. Model fit was assessed using the variance inflation factor $\hat{c}$ (calculated as the residual deviance divided by degrees of freedom) of the global (fully parameterized) model – values close to 1 indicate a well-fitting model (Burnham & Anderson 2002). Finally, to ensure that no important variables had been excluded during preliminary analysis, we tested for reductions in AIC score upon addition of excluded terms to the best model for each month. We also tested for curvilinear relationships between response and predictor variables by assessing changes in AIC following the addition of quadratic terms for each variable to the best model.

Field-scale habitat associations

Although individual pairs may range over areas significantly larger than individual fields, the lack of colour-marked birds in our study area prevented the delimitation of entire home-ranges. Rather, field-scale models were constructed using estimates of the maximum number of territories recorded in each field in the intensive field-scale survey. Models therefore may not be representative of all habitat selection decisions made in selecting home ranges, for example foraging habitats (Gilroy *et al.* 2009), but are likely to provide a reliable indicator of crop selection for nesting. To increase the range of crop types sampled, we also constructed separate models using field-scale territory counts from all fields surveyed during the 2004 large-scale transect survey. In both cases, GLM models were fitted to territory counts for each field surveyed, including fixed-effect terms for crop type and field size (truncated to the zone encapsulating 95% of Yellow Wagtail detections for the transect survey), as well as a random factor denoting the study site or transect to which each field belonged, accounting for differences in the availability of crops between transects and sites. Crop associations were determined by comparison of model coefficients relative to a reference category set to unity (the category 'other' which included all rarer crop types). These analyses were performed using the GLIMMIX macro in SAS version 8.02 (SAS Institute Inc., 2001).

In order to test for differences in detection rate of Yellow Wagtails at the field scale in relation to time of day, season and crop type, distance-detection functions were fitted using the program DISTANCE 5.0 Release 2 (Thomas *et al.* 2006). Each variable was included as a categorical covariate (with time of day divided into 3-h bands), with differences in the scale and shape of detection functions being assessed by visual appraisal.

Breeding success

Habitat-specific estimates of nest survival likelihood were calculated using the Mayfield method (Mayfield 1975), which combines the rate of nest failure with the number of days in which active nests are monitored, thereby correcting for bias resulting from nests within the study area failing prior to their discovery. Variance and standard errors of the estimate were calculated using methods described by Johnsson (1979). Clutch size, brood size at fledging and daily nest survival likelihood were compared across crop types using generalized linear models (Aebischer 1999). Models included terms for study site and date of nest initiation to control for unmeasured large-scale spatial and temporal variation. Clutch size and unpredated brood size were modelled specifying Poisson errors and log-link function, whilst nest survival likelihood was modelled using a binomial error distribution and logit link function. For survival likelihood models, the response variable was nest predation (1) or survival (0), with the number of nest-exposure days between detection and outcome as the binomial denominator. For each breeding success component, the magnitude of variation between crop types was determined by assessing the change in residual deviance following the removal of the crop term from the model via a likelihood ratio test, with significance assessed by comparison with the Chi-squared distribution with the appropriate number of degrees of freedom (Crawley 1993).

RESULTS

Large-scale habitat associations

Territorial Yellow Wagtails were recorded across the study region, and there was no evidence of a seasonal decline in the number of territorial birds, with a mean of 1.09 territories per transect in May, 1.29 in June and 1.18 in July. The proportion of adult birds recorded that were not engaged in territorial activity (as defined above) during observation was 0.216 in May, 0.280 in June and 0.284 in July, suggesting that the proportion of adult birds involved in territorial or breeding activity remained broadly similar throughout the survey period. The distribution of Yellow Wagtails changed during the course of the breeding season, as shown by the abundance of territorial birds at individual transects across the 3 months (Fig. 2).

Yellow Wagtails were widely distributed during early stages of the season, with territories occurring along 52.5% of transects in May. However, during June and particularly in July, territorial birds became concentrated in certain areas and simultaneously disappeared from others, resulting in a significant change in the distribution of territories per transect between May and July (Kolmogorov–Smirnov test $D = 0.164$, $P = 0.045$). Territories were recorded at 50.5% of transects in June and 40.8% in July, indicating an increase in the spatial clumping of territories. The same pattern was found when all records of adult Yellow Wagtails were considered (including individuals not engaged in territorial or breeding activity during observation), with individuals being recorded at 56.1% of transects in May, 52.2% in June and 42.4% in July. Distance–detection functions were similar between months, with detection rates being relatively uniform at perpendicular distances up to 150 m, declining significantly thereafter (proportion of detections < 150 m in May = 92.2%, June = 95.1%, July = 94.8%). Detection functions were also similar across all time of day categories.

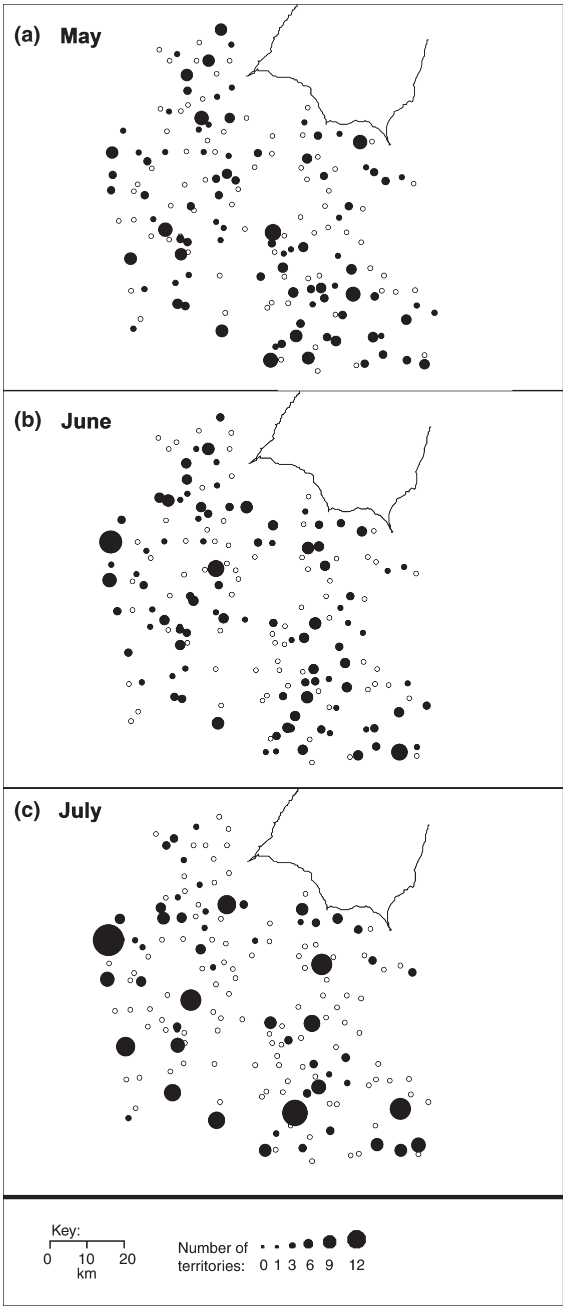

Figure 2. Counts of Yellow Wagtail territories recorded on 190 transects in arable farmland during May, June and July in eastern England. Each point represents the number of territorial pairs recorded on a single transect, located at the circle midpoint. Line indicates the North Sea coastline.

Changes in the distribution of territorial Yellow Wagtails were associated with a shift in habitat association away from autumn-sown cereals and towards potato crops. Hierarchical partitioning analysis showed that the area of autumn-sown cereals made the most significant independent contribution to Yellow Wagtail abundance on transects in May, followed by area of hedges, crop diversity, area of potatoes and soil type (Table 2). In June, area of potatoes made the most significant contribution, followed by area of hedges, crop diversity and soil type. In July, area of potatoes was again the most significant contributor, followed by crop diversity, area of unvegetated margin and area of hedge. The results were similar when the monthly analyses were repeated using response variables that included both territorial and non-territorial adults, with identical ranking of predictor variables and only small changes in model coefficient values.

The 10 best-fitting models predicting territory abundance at the transect scale are shown in Table 3, ranked according to their AIC score. In all months, the best models retained all the variables found to be significant in the hierarchical partitioning analysis. Addition of variables that were excluded in previous stages of analysis did not improve the fit of any of the best models. Similarly, addition of polynomial terms did not improve fit, implying that all relationships with predictor variables were linear. Furthermore, addition of polynomial terms for variables that were not significant as linear predictors did not improve model fit in any case. Akaike weights for the best models were all above 0.7, suggesting strong support for the predictive performance of the best models. However, in May and June, several candidate models were within 6 AIC points of the best model, suggesting some uncertainty in model selection (Burnham & Anderson 2002). Consequently, we calculated model-averaged regression coefficients for each variable (Burnham & Anderson 2002), weighted by model Akaike weights, shown in Table 4. Positive associations with potatoes and crop diversity were consistent through all months, and the strength of both relationships increased as the season progressed. The negative relationship with the area of hedges was also consistent across months. The positive association with area of autumn-sown cereals was only apparent in May, and the variable was not retained in any later models. Similarly, a positive association with the area of bare field margins was only apparent in July. Soil associations were consistent in both May and June, with peaty soils being favoured most strongly, followed by loams, clay soils, silty soils and sandy soils. In July, soil type did not have any independent effect on Yellow Wagtail abundance and therefore was not retained in the model.

Field-scale habitat associations

The distribution of territorial and breeding individuals at the field scale strongly supported the transect-level predictors of abundance for each month. Modelling territory abundance across all fields surveyed by the large-scale 2004 transect survey revealed that most observations of territorial individuals in May were from autumn-sown cereal

Table 2. Results of hierarchical partitioning analysis, showing the relative influence of habitat variables on Yellow Wagtail territory abundance across 190 transects in eastern England. The *Z* score indicates the independent contribution of each variable to model goodness of fit, in comparison with the results of 1000 randomizations, with significance based on the upper 0.95 and 0.99 confidence limits. Note that negative *Z* values indicate negligible contribution to model fit, rather than negative relationships.

Variable	May	June	July
Autumn cereals	7.92**	0.92	0.09
Spring cereals	0	1.18	0
Field beans	0.22	1.12	1.45
Peas	0	−0.15	−0.03
Potatoes	3.19*	8.38**	23.39**
Sugar beet	0.1	0	−0.29
Wet ditch	0.25	0.6	0.35
Bare margin	−0.11	−0.62	4.12*
Hedge	4.21*	3.59*	3.35*
Buildings	0.5	0	0.69
Crop diversity index	2.33*	3.07*	6.96**
Soil type (CAT)	1.95*	2.1*	0.64

*Parameter effects significant at $P < 0.05$, **significant at $P < 0.01$ tested by randomization.

Table 3. Results of model selection using AIC for generalized linear models of Yellow Wagtail territory abundance across 190 transects in eastern England. The 10 best ranked models are listed for each month, together with their Akaike weights (AIC_w). For each month, competing models included only those variables found to have an independent effect on Yellow Wagtail abundance in hierarchical partitioning analysis.

	May			June			July		
Rank	Model	AIC	AIC_w	Model	AIC	AIC_w	Model	AIC	AIC_w
1	wcer + pots + hedge + soil + cropdiv	543.1	0.705	pots + soil + hedge + cropdiv	532.4	0.722	pots + baremar + hedge + cropdiv	501.5	0.978
2	wcer + hedge + soil + cropdiv	546.1	0.154	pots + soil + hedge	534.5	0.261	pots + hedge + cropdiv	509.2	0.022
3	wcer + pots + hedge + cropdiv	547.8	0.066	pots + soil + cropdiv	540.8	0.011	pots + baremar + cropdiv	515.9	0.001
4	wcer + pots + soil + cropdiv	548.3	0.051	pots + soil	543.2	0.003	pots + cropdiv	520.0	< 0.001
5	wcer + soil + cropdiv	551.1	0.013	pots + hedge + cropdiv	543.8	0.002	pots + baremar + hedge	532.3	< 0.001
6	wcer + pots + hedge + soil	552.2	0.007	soil + hedge + cropdiv	546.8	0.001	pots + hedge	540.5	< 0.001
7	wcer + hedge + cropdiv	554.1	0.003	pots + hedge	547.8	< 0.001	pots + baremar	543.9	< 0.001
8	wcer + pots + cropdiv	556.5	0.001	soil + hedge	551.0	< 0.001	pots	548.6	< 0.001
9	wcer+pots + soil	557.0	0.001	pots + cropdiv	551.5	< 0.001	baremar + hedge + cropdiv	577.0	< 0.001
10	wcer + hedge + soil	560.4	< 0.001	pots	532.4	< 0.001	baremar + cropdiv	604.8	< 0.001

wcer, area of autumn-sown cereal; pots, area of potatoes; hedge, hedge basal area; soil, soil category; cropdiv, crop diversity index (Simpson's R); baremar, area of bare margin.

fields, but use of this crop declined in June and fell to almost zero in July (Table 5). Occupancy rates in June and July were highest in potato crops, and were also relatively high in field beans and pea crops, whereas sugar beet and other vegetable crops supported smaller numbers of territories (Table 5). Patterns of crop association remained unchanged when model selection was repeated using all sightings of adult birds (including foraging individuals). Visual appraisal of distance–detection functions suggested that there were no marked differences between crops, each showing a consistent decline in detection above 150 m, although the possibility of crop-related differences in detection likelihood cannot be discounted statistically.

In intensively surveyed sites in 2005, models of territory preference at the field scale indicated a strong association with autumn cereal crops in May, but this declined significantly in June and July (GLMM parameter coefficients and standard errors: May = 1.869 ± 0.453, June = 1.324 ± 0.229, July = −0.201 ± 0.456). Occupancy of potato crops was low in May but increased significantly in June, and by July the great majority of territories were located in this crop (GLMM parameter coefficients and standard errors: May = −4.351 ± 5.106, June = 2.490 ± 0.304, July = 4.355 ± 0.268). On the three sites that lacked potato fields, total observations of Yellow Wagtails (including apparently non-territorial individuals) declined to almost zero in July, whilst observations of both territorial and non-territorial individuals remained stable or increased on sites where potato crops were present (Table 6).

Breeding success

A total of 89 nests were found and monitored during the intensive study in 2005, all being located within crop fields. Most nests were found in autumn-sown cereals ($n = 25$) and potatoes ($n = 48$), with small numbers also found in peas ($n = 3$) and field beans ($n = 13$). Sample sizes were insufficient to analyse crop-specific success rates separately for egg and chick stages, so data were pooled across the entire nest period. There was no significant difference in daily nest-survival rate between the two main crops used ($\chi^2 = 1.314$, df = 1, $P = 0.189$). The likelihood of surviving to fledge at least one offspring was 0.332 (±0.091 se) in autumn cereals and 0.350 (±0.101 se) in

Table 4. Parameter estimates from generalized linear modelling of Yellow Wagtail territory abundance across 190 transects in eastern England. Coefficients are average across all competing model combinations, weighted by their AIC score, together with unconditional standard errors, as well as an indication of the direction of the association. Selection probabilities show the likelihood that each variable has a genuine effect on territory abundance, derived by summing Akaike weights for all models containing that variable. Coefficient estimates for soil categories are relative to reference category 'clay', which is set to zero.

	May		June		July	
Variable	Coefficient	Selection probability ($\sum \mathrm{AIC}_w$)	Coefficient	Selection probability ($\sum \mathrm{AIC}_w$)	Coefficient	Selection probability ($\sum \mathrm{AIC}_w$)
Winter cereals	0.004 ± 0.001 (+)*	> 0.999	–	–	–	–
Potatoes	0.002 ± 0.001 (+)*	0.829	0.004 ± 0.001 (+)*	> 0.999	0.007 ± 0.001 (+)*	> 0.999
Bare margin	–	–	–	–	0.001 ± 0.011 (+)	0.978
Hedge	0.076 ± 0.023 (−)*	0.935	0.005 ± 0.001 (−)*	0.986	0.002 ± 0.002 (−)	> 0.999
Crop diversity	1.637 ± 0.446 (+)*	0.992	0.571 ± 0.488 (+)*	0.737	2.593 ± 0.621 (+)*	> 0.999
Soil type						
Loam	0.156 ± 0.227 (−)	0.931	0.456 ± 0.310 (+)*	0.997	–	–
Peat	0.285 ± 0.055 (+)*	0.931	0.791 ± 0.255 (+)*	0.997	–	–
Sand	0.590 ± 0.113 (−)*	0.931	0.518 ± 0.104 (−)*	0.997	–	–
Silt	0.150 ± 0.128 (−)*	0.931	0.446 ± 0.361 (−)*	0.997	–	–
Clay	0	0.931	0	0.997	–	–

*Denotes coefficients with error margins that do not include zero.

Table 5. Crop associations of territorial Yellow Wagtails at the field scale across 190 transects, during 3 months spanning the UK breeding season. Relative association values are model coefficients from a generalized linear mixed model of number of territories per field. Crop (categorical) was included as a fixed effect, with transect number modelled as a random effect. Note that field size (ha) was also included in the model as a fixed effect (with values truncated to within the effective sampling distance of 300 m). All values are relative to the reference category 'Other', which was set to zero. Values are given with their standard error, as well as an indication of the direction of the association. Density values give the number of territories recorded per km^2 surveyed of each crop per month. The total number of territories recorded in each crop type is also given.

	May			June			July		
Crop	Relative association	Density (territories/km^2)	Total territories	Relative association	Density (territories/km^2)	Total territories	Relative association	Density (territories/km^2)	Total territories
Autumn cereal	0.17 ± 0.06 (+)*	2.67	162	0.14 ± 0.05 (+)*	2.24	127	0.03 ± 0.05 (−)	0.37	13
Spring cereal	0.07 ± 0.07 (+)	1.90	5	0.09 ± 0.08 (+)*	2.03	5	0.01 ± 0.09 (+)	0.57	1
Oilseed rape	0.13 ± 0.06 (−)*	0.13	1	0.09 ± 0.07 (−)*	0.00	0	0.06 ± 0.08 (−)	0.00	0
Field beans	0.01 ± 0.07 (−)	0.76	3	0.27 ± 0.08 (+)*	3.59	13	0.48 ± 0.09 (+)*	10.01	21
Peas	0.12 ± 0.06 (+)*	2.18	13	0.28 ± 0.06 (+)*	4.15	26	0.24 ± 0.09 (+)*	4.81	22
Potatoes	0.02 ± 0.04 (+)	1.17	9	0.51 ± 0.05 (+)*	8.47	64	1.21 ± 0.06 (+)*	23.35	144
Sugar beet	0.06 ± 0.04 (−)*	0.08	1	0.04 ± 0.04 (−)	0.18	2	0.04 ± 0.05 (+)	2.19	16
Vegetables	0.13 ± 0.09 (+)*	3.47	8	0.04 ± 0.08 (+)	1.39	4	0.04 ± 0.07 (+)	1.20	5
Set-aside	0.03 ± 0.05 (+)	0.91	4	0.01 ± 0.06 (+)	0.48	2	0.01 ± 0.07 (+)	0.00	0
Other	0	0.31	1	0	0.36	3	0	0.67	4

*Denotes variable coefficients with error margins that do not include zero.

potatoes. Similarly, models showed no significant difference in clutch size ($\chi^2 = 1.54$, df = 1, $P = 0.405$; autumn-sown cereal mean 4.885 ± 0.151 se; potatoes mean 4.312 ± 0.140 se), and although mean brood size at fledging was lower for nests in potato crops than in cereals (autumn-sown cereal mean 4.450 ± 0.220 se; potatoes mean 3.517 ± 0.219 se), the change in model deviance after removing the crop term was not statistically significant ($\chi^2 = 2.65$, df = 1, $P = 0.103$).

Table 6. Seasonal changes in relative abundance of Yellow Wagtails across six intensive field-scale survey sites in Lincolnshire and Cambridgeshire in 2005. Sites were surveyed twice a month using territory mapping methodology. Territories were identified on the basis of a suite of behaviours indicating breeding activity (see Methods). Total observation densities are derived from mean number of sightings of adult Yellow Wagtails per survey visit during each month. Crop areas are shown only for the principal crops used for nesting – potatoes and autumn cereals.

	Yellow Wagtail density (territories/km and total observations of adults/km)						Area (ha) of		
	May		June		July				
Site	Territories	Total obs.	Territories	Total obs.	Territories	Total obs.	Potatoes	Autumn cereal	Whole site
Bourne South Fen	7.5	11.4	8.3	12.5	8.6	10.4	98	186	610
Borough Fen	4.8	7.6	5.3	6.2	4.0	6.7	47	129	442
Langtoft Fen	8.3	10.7	4.8	11.3	3.9	7.4	22	142	395
Archer's Drove	3.3	5.1	3.4	7.1	0.8	1.8	0	229	524
Deeping Fen	3.4	4.0	4.7	7.8	0.9	1.6	0	215	453
Dunsby Fen	1.6	3.0	3.4	4.8	0.7	1.5	0	372	920

DISCUSSION

At both regional and local scales, there was a marked shift in the breeding distribution and habitat associations of Yellow Wagtails during the course of the breeding season. Whilst overall numbers of breeding Yellow Wagtails remained similar throughout the breeding period, their distribution shifted in response to a change in the crop types selected for breeding. During the early season, most territories and nests were located in autumn-sown cereal fields, but this crop was largely abandoned as the season progressed, with other crops (particularly potatoes) becoming more strongly favoured, echoing patterns of crop preference observed in German arable landscapes (Stiebel 1997). Intensive territory-mapping revealed that study areas lacking suitable late-season breeding habitats were largely abandoned by Yellow Wagtails during the latter part of the season, whilst numbers remained stable or increased on sites supporting preferred late-season habitats (particularly potato crops). Large-scale transect surveys revealed that this pattern occurred throughout our study region, implying that widespread mid-season breeding dispersal was taking place, although the possibility of earlier migratory departure by early breeders cannot be fully discounted. Other habitat features influencing territory abundance included soil type, local diversity of cropping and the presence of hedges.

Mid-season habitat association shifts

Previous studies have shown that colour-ringed Yellow Wagtails move up to 1 km between successive breeding attempts (RSPB, unpubl. data), and much larger movements may be possible depending on the time available for breeding prior to autumn migration, as well as other costs such as energetic stress and predation risk (Sutherland *et al.* 2000, Dale *et al.* 2006). As the total number of adult Yellow Wagtails recorded during the large-scale transect survey was similar throughout the study period, it seems likely that the observed shift in distribution resulted from breeding dispersal away from initial territories. The pattern of abundance observed over our field-scale study sites further supports this hypothesis, with Yellow Wagtails largely disappearing from sites that lacked potato cropping during the latter part of the season. Alternatively, this pattern could be explained if the establishment of late-season territories involved immigration by 'floaters' that had failed to attain early territories (Zack & Stutchbury 1992, Pen & Weissing 2000), with early nesters simply ceasing breeding activity and commencing migration. However, our habitat association model results were similar whether we included only territorial individuals or all sightings of adult birds, suggesting that seasonal changes in habitat associations were consistent throughout the study population.

By performing mid-season breeding dispersal, individuals might increase their likelihood of successfully raising two broods, or at least raise replacements for failed early broods, after habitat in their initial territory has become unfavourable (Stiebel 1997). Our measures of reproductive success suggest that breeding output was similar in both early nests in autumn-sown cereals and late nests in potatoes, implying that late nests could make a significant contribution to annual reproductive success. However, the extent to which this pattern influences productivity at a population scale within arable habitat remains unknown, as we were not able to assess the proportion of individuals attempting second broods. Nevertheless, our results imply that the effects of local declines in habitat suitability in autumn cereals could be buffered at least locally by the use of alternative habitats (Sol *et al.* 2002). Speculatively, the positive relationship with potato crops observed at the transect level in May (i.e. before this crop is suitable for nesting) might indicate a higher broad-scale abundance of Yellow Wagtails in areas where potatoes are grown, tentatively supporting the possibility of a population-scale effect. The shift in habitat associations shown by Yellow Wagtails could indicate an endogenous change in the type of vegetation structure preferred for nesting (Soderstrom 2001). However, it is perhaps more likely that the underlying habitat preference decision rules remain unchanged, but are triggered by different habitats sequentially as they reach appropriate growth stages during the course of the season.

Other habitat associations

In both May and June, soil type was a significant predictor of Yellow Wagtail abundance. Soils are a fundamental determinant of agricultural practices, and consequently influence various farm characteristics (Bauer & Black 1994, Lal 1998). Many of these soil-related characteristics correlate with Wagtail abundance in turn, and as such, soil type may be an effective indicator of habitat suitability by encapsulating a range of habitat features, particularly cropping patterns. However, the retention of soil type in our models ahead of many other farm-related variables might imply a more proximate influence of soils on Yellow Wagtail habitat selection. Organic content, in particular, may be important as soil types with higher levels of organic matter (peat and loam) showed a stronger association with Yellow Wagtail abundance. This echoes the results of a related study of field-scale habitat selection within the region, in which Yellow Wagtail abundance was found to be closely related to local variations in soil penetrability (Gilroy *et al.* 2008), a feature that is positively correlated with organic content (Huntington *et al.* 1989, Da Silva *et al.* 1997).

Relationships between soils and farmland bird distributions are seldom documented, although a small number of cases have been reported (e.g. Lister 1964, Green *et al.* 1990, Wilson *et al.* 2005). In addition to their influence on overall cropping patterns, soils may be a significant determinant of prey abundance for insectivorous birds, as soil organic content is known to influence a variety of invertebrates, including springtails (Larsen *et al.* 2004), beetles (Gudleifsson 2005) and spiders (Gudleifsson & Bjarnadottir 2004). The influence of soil type on important prey groups for Yellow Wagtails, such as flies and damselflies (Roselaar 1988), is yet to be determined.

Yellow Wagtails were also found to be negatively associated with hedges, measured as total length bordering fields adjacent to each transect, supporting previous studies that demonstrate a preference for open landscapes of this species (Dittberner & Dittberner 1984, Stiebel 1997, Mason & Macdonald 2000). The lack of consistent associations with other field boundary types, such as wet ditches, is perhaps surprising. The latter are a common habitat feature in the study region, and are likely be an important source of prey for Yellow Wagtails, particularly damselflies (Wilson *et al.* 1999). However, almost all ditches in the region are steep-sided (*c.* 45°) with heavily vegetated banks. They are rarely used as foraging sites by Wagtails, which prefer open areas where movement and prey detection are unimpeded (Smith 1950, Bradbury & Bradter 2004). Thus, although ditches may be a major determinant of invertebrate biomass at a landscape level, any more local effect on Yellow Wagtail abundance was not detected at the scale of our survey. Overall crop diversity was found to be a strong positive predictor of breeding abundance throughout the season, potentially indicating a preference for landscapes comprising a variety of vegetation heights and structures, in which multiple breeding opportunities could arise over the course of a season. Landscape-level habitat diversity is known to be important in maintaining farmland bird biodiversity across Europe by providing a greater range of nesting and foraging opportunities throughout the season (Stoate *et al.* 2001, Benton *et al.* 2003).

Conservation

This study has highlighted the possibility that breeding dispersal and a change in habitat use play a role in buffering the effects of within-season habitat change. The results underline the potential for patterns of habitat use to change during the course of a season; this possibility should be borne in mind in the design of future studies aimed at determining the ecological requirements of target species, particularly in seasonally variable agricultural environments. For the suite of multi-brooded farmland species that are known to be influenced by seasonal changes in habitat suitability (see Newton 2004), plasticity in habitat use and site fidelity could play an important role in determining annual breeding productivity.

The availability of suitable late-season nesting habitat has a strong influence on the distribution of Yellow Wagtail breeding pairs at a landscape scale. In many farmed landscapes, crop diversity is limited to a small number of economically profitable crop alternatives, and suitable late-season breeding habitats (such as potatoes) may be unavailable within the dispersal range of Yellow Wagtails, leading to the early curtailment of breeding activity. Conservation measures for this declining species in arable farmland should include the provision of suitable late-season habitats (i.e. with a vegetation structure and phenology analogous to a potato crop) within low-diversity arable landscapes. Options within the existing English agri-environment entry-level scheme, for example option 'EF6' (spring cropping/overwinter stubbles), may provide suitable late-season resources if appropriate crops are selected. Further study of the late-season use of fields under this option by Yellow Wagtails is desirable. Studies of season-long habitat use and dispersal distance among birds and other mobile taxa are likely to enhance our understanding of the way organisms respond to temporal changes within agricultural environments.

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