



Effects of seed-rich habitat provision on territory density, home range and breeding performance of European Turtle Doves *Streptopelia turtur*

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(Received 19 May 2020; revision accepted 29 October 2020)

Summary

Conservation measures providing food-rich habitats through agri-environment schemes (AES) have the potential to affect the demography and local abundance of species limited by food availability. The European Turtle Dove *Streptopelia turtur* is one of Europe's fastest declining birds, with breeding season dietary changes coincident with a reduction in reproductive output suggesting food limitation during breeding. In this study we provided seed-rich habitats at six intervention sites over a 4-year period and tested for impacts of the intervention on breeding success, ranging behaviour and the local abundance of territorial turtle doves. Nesting success and chick biometrics were unrelated to the local availability of seed-rich habitat or to the proximity of intervention plots. Nestling weight was higher close to human habitation consistent with an influence of anthropogenic supplementary food provision. Small home ranges were associated with a high proportion of non-farmed habitats, while large home ranges were more likely to contain seed-rich habitat suggesting that breeding doves were willing to travel further to utilize such habitat where available. Extensively managed grassland and intervention plot fields were selected by foraging turtle doves. A slower temporal decline in the abundance of breeding males on intervention sites probably reflects enhanced habitat suitability during territory settlement. Refining techniques to deliver sources of sown, natural, and supplementary seed that are plentiful, accessible, and parasite-free is likely to be crucial for the conservation of turtle doves.

Keywords: agri-environment, conservation intervention, food supplementation, habitat provision, *Streptopelia turtur*, supplementary feeding

Introduction

Food availability is a key limitation for animal population size (Lack 1954, Martin 1987, Arcese and Smith 1988), and can influence territory size (Arvidsson *et al.* 1997), laying date and reproductive success (Arcese and Smith 1988). Many endangered or declining populations are food-limited as a

result of habitat degradation or other anthropogenic activities such as pesticide use (e.g. Boatman *et al.* 2004, Hart *et al.* 2006). Efforts to increase food availability can improve breeding success, whether through the provision of foraging habitat at a broad scale (Baker *et al.* 2012, Bright *et al.* 2015), or through supplementary feeding (Castro *et al.* 2003, Schoech *et al.* 2007).

Direct supplementation, the provision of food (i.e. seed provided anthropogenically rather than on a growing plant), is a straightforward management intervention and, where food is limiting, generally has rapid, positive effects on breeding success (Castro *et al.* 2003, Schoech *et al.* 2007, Ruffino *et al.* 2014). However, supplementary feeding may also have unexpected detrimental side-effects (e.g. Blanco *et al.* 2011) and, in some species, may even reduce productivity (Harrison *et al.* 2010, Plummer *et al.* 2013). Consequently, food supplementation for conservation management tends to be recommended as a short-term solution where, for example, a prey population is recovering from a population crash (López-Bao *et al.* 2008), although for some translocated or heavily managed populations, long-term supplementary food provision may be necessary (Castro *et al.* 2003). Additional, undesired side-effects can include the concentration of predators, or increased transmission of pathogens and parasites (Schoech *et al.* 2007, Tollington *et al.* 2015), which can undermine the positive effects of food supplementation (Blanco *et al.* 2011).

Longer-term solutions to food shortage over a wider scale can be implemented through land management schemes, which can positively impact populations of widespread declining birds (Bright *et al.* 2015). Within farmland habitats, agri-environment schemes (AES) provide payments (based on the profit-forgone plus the costs of management) to farmers who modify their cropping and/or provide non-cropped habitat through various options designed to provide either nesting or seed/insect-rich foraging habitats for birds. In England, there is strong evidence for positive effects of management that provides seed food resources (e.g. stubble and wild bird seed mixes) on population growth rates across multiple granivorous species, at different landscape scales (Baker *et al.* 2012).

The European Turtle Dove (hereafter Turtle Dove) is one of Europe's fastest declining breeding birds (-80% since 1980; PECBMS 2019). Within the UK, population declines have been linked to a reduced reproductive effort and a curtailing of the breeding season (Browne and Aebischer 2004), occurring concurrently with a dietary switch from broad-leaved arable plants to mainly cultivated crops (Browne and Aebischer 2003). Turtle Doves are obligate granivores, favouring weedy areas of sparse vegetation cover as foraging habitat and the reduction in such areas, along with a decline in previously widespread arable plants such as common fumitory *Fumaria officinalis* (Potts *et al.* 2010), suggests that food may now be limiting for this species. This is supported by our recent findings of a novel use of anthropogenic food likely provided by householders for garden birds in Turtle Dove diet (Dunn *et al.* 2018). The continued population decline and evaluation of AES in the UK suggests current interventions may not be providing sufficient suitable foraging habitat, in terms of either food abundance or accessibility, to support the Turtle Dove population (Dunn and Morris 2012). Recent findings show positive effects of seed-rich habitat on post-fledging survival in this species (Dunn *et al.* 2017) but the high prevalence of the protozoan parasite *Trichomonas gallinae*, which has been linked to mortality in both adult and nestling Turtle Doves (Stockdale *et al.* 2015), in *ex-situ* seed piles (Thomas 2017) and other columbids (Lennon *et al.* 2013) made the standard methods of supplementary seed provision available at the time of this study (e.g. through options in the English Environmental Stewardship AES; Natural England 2012a, 2012b) unsuitable for Turtle Doves, even as a short-term solution. Consequently, we developed a conservation intervention designed to provide an *in-situ* source of seed food for Turtle Doves throughout the breeding season (Dunn *et al.* 2015). Here, we determine whether our intervention positively impacts Turtle Dove reproduction or breeding density.

First, we test whether our intervention influences the abundance of territorial male Turtle Doves at the farm scale over a five-year period. Second, for our intervention together with a suite of potentially beneficial AES options, we test whether the provision of seed-rich habitat influences the ranging behaviour or reproductive success of Turtle Doves on farmland.

Methods

Study sites and the provision of seed-rich intervention plots

Data collection was conducted at 12 sites per year spread across Essex, Suffolk, Cambridgeshire, and Norfolk in the east of England. Sites were selected during summer 2010 on the basis of the presence of at least two territorial Turtle Doves within a 1-km square dominated by arable farmland, with no more than 5% of the land area across the whole farm (not just the focal 1-km square) comprising seed-rich, non-cropped habitats such as fallow or wild bird seed mixes. This was to increase the likelihood that any effect of seed-rich habitat was due to intervention plots rather than pre-existing habitats. During 2011 and 2012, six intervention sites were established, each sown with 4–7 plots totalling 2 ha of a seed-rich mix ('intervention plots') designed to provide a source of seeds present in Turtle Dove diet, throughout the breeding season (Table S1 in the online supplementary material); the remaining six sites received no intervention management and served as control sites (Dunn *et al.* 2015). During 2013–2014, a modified seed mix, changed to improve vegetation structure and seed accessibility (Table S1), was sown at four of the existing intervention sites. Five new control and two new intervention sites were recruited using the same criteria as previously because Turtle Doves had become either scarce or absent at the original sites (Table S2).

Site status initially reflected the presence or absence of intervention plots ('desired status'). However, vegetation structure on some sown plots was too tall and dense to allow access to foraging doves (Dunn *et al.* 2015), and one control site from 2011–2012 was found to have a sown strip of common fumitory in 2014, thus providing the vegetation structure and seed availability for which intervention plots had been designed. We therefore defined a second site status variable ('actual'), which described the presence or absence of accessible sown intervention plots (including fumitory) for Turtle Doves (summarised in Table S2).

Surveys of territorial males

Field surveys aimed to detect the presence and abundance of singing male Turtle Doves at each site, where the site consisted of the entire farm rather than just the focal 1-km square (Mean \pm 1 SE site area: 1.72 ± 0.31 km²). Each active intervention and control site was surveyed twice during each year of the study (2011–2014), once early in the breeding season (between mid-May and the end of the first week in June), and once later (mid–late June) to detect late-settling males. Field surveys followed the method of Dunn and Morris (2012) and involved the observer walking two parallel 1-km transects recording all Turtle Doves. Transects began at sunrise and lasted a maximum of two hours as Turtle Dove vocal activity falls markedly thereafter (Calladine *et al.* 1999).

Turtle Dove capture and radio-tagging

Turtle Dove capture was attempted at all sites using mist nets and whoosh nets (Redfern and Clark 2001) at locations temporarily baited with wheat, oil seed rape or a commercial bird mix (details in Stockdale *et al.* 2015). We caught birds in Essex and Norfolk only: 15 birds at five sites during 2011–2012, and 38 birds at seven sites during 2013–2014. Once caught, birds were sexed where possible according to plumage colouration and aged as either adult (hatched the previous year or before) or juvenile (Baker 1993). Adults were fitted with a 1.7 g PicoPip radio-tag (Biotrack, Dorset, UK) glued to the central tail feathers and secured with dental floss. Tags had a line-of-sight range of up to 6 km and a ground-ground range of up to 600 m.

Following release, each bird was relocated as soon as possible in order to determine whether it was nesting. Subsequently, to minimise spatial correlation between consecutive tracking fixes, we divided the day into six 3-hour periods (between 04h00 and 22h00) and within each 5-day period we attempted to relocate each bird on at least one occasion during each 3-hour period (Browne and Aebischer 2003). We obtained fixes by taking 3–5 bearings and calculating the central point of the

overlap zone. To obtain each fix, we started searching for the bird in the vicinity of the nest site using a car-mounted aerial and then within concentric buffer zones around the nest up to 5 km from the nest. We excluded from the analysis any fixes for which points did not converge, or for which the observer was more than 1 km from the predicted location of the bird.

Nest location and breeding parameters

Turtle Dove nests were found by monitoring the movements of tagged birds as well as cold-searching habitat known to contain territorial males. Once found, nests were checked every 2–3 days, recording numbers of eggs or live chicks present and estimating chick age from plumage. Nest success was inferred from an empty and undamaged nest where the young were old enough to have fledged since the previous visit, or the presence of recently fledged young nearby. Nest failure was either known (nest contained cold eggs, egg fragments or dead chicks) or was inferred from an empty nest on a date prior to a plausible fledging date, often with chick remains visible near or underneath the nest. For analytical purposes, the date of failure was assumed to be the mid-point between the last two visits. First egg date (FED; a day-specific integer where 1 = 1 May) was deduced from incomplete clutches, known hatch dates and estimated chick ages. Nest habitat was categorised as within either a linear feature (hedgerow) or a non-linear habitat patch (scrub), and height of the nest platform above ground was measured (± 5 cm). Nest vegetation cover was measured using an upwards-facing fish-eye lens camera within three days of a nesting attempt ending. Images were subsequently analysed using Gap Light Analyser (Frazer *et al.* 1999) to derive the percentage of sky visible in the image. When nestlings were seven days old, they were weighed using a digital balance (± 0.1 g) and their tarsus measured using Vernier callipers (minimum tarsus ± 0.1 mm; Redfern and Clark 2001). Ideally, we would have measured the number of breeding attempts per pair per season as we expected to catch birds at the earliest stages of nesting; however, some birds were found to be at late stages of nesting when relocated shortly after radio-tagging relatively early in the season, and thus we could not be certain of including nesting attempts that may have occurred prior to radio-tags being fitted to estimate season-long productivity.

Home range

Radio-tracking fixes further than 50 m of the nest, which we assumed were likely to be foraging locations, were used to estimate adult home ranges for the incubation and chick stages separately. Minimum convex polygons (MCPs) were calculated for each adult nesting attempt stage with more than five qualifying locations (mean \pm SE fix number: 10.82 \pm 0.63; incubation stage: 31 nests from 22 birds; chick stage: 21 nests from 18 birds). We used 90% MCPs to define the core foraging range of each bird because including all fixes considerably inflated MCPs (mean \pm SE home range at each % MCP (ha): 100%: 186.58 \pm 32.00; 90%: 86.09 \pm 16.38; 80%: 56.37 \pm 13.79; 70%: 36.57 \pm 11.54).

Measuring habitat availability

We quantified habitat availability within each home range as potential predictors of breeding performance. During 2013 and 2014, we mapped field-scale habitat within 3 km of each Turtle Dove nest, as well as around any more distant foraging areas located through radio-tracking. These data were digitised using ArcMap 10.1 and the habitat within each 90% MCP calculated using the 'gIntersection' command in the *rgeos* package (Bivand *et al.* 2014). All statistical analyses were carried out in R version "Pumpkin helmet" for Mac (R Core Team 2016). Within each 90% MCP we calculated the proportions of cereal and oilseed rape, along with the ratio of grass to arable land. Using Rural Land Registry data, we also calculated the proportion of non-farmed land within each MCP. Non-farmed habitat lies outside land upon which Basic Payment Scheme (BPS) payments are claimed and in our study areas comprised areas of mainly woodland and scrub, quarries, amenity

land and “seed rich” habitats such as fallow, semi-natural grassland and low intensity horse pastures (any standing water or urban areas were excluded from the area of non-farmed habitat; Table 1). We calculated the distance of each nest to the nearest intervention plot providing accessible habitat, the nearest semi-permanent standing water source (known to influence territory retention; Dunn and Morris 2012) and the nearest inhabited building (as a surrogate for the availability of provisioned food such as bird seed mix in gardens) (± 5 m) using digitised 1:10,000 GB Ordnance Survey maps. Data on the extent of AES options likely to provide suitable foraging habitat for Turtle Doves were provided by Natural England. Option areas were weighted by the expected seed abundance and accessibility to foraging doves to calculate an index of available seed-rich habitat within farmed areas (or ‘seed index’; Table S3).

Changes in Turtle Dove abundance

To determine whether changes in the abundance of territorial Turtle Doves differed between intervention and control sites, we fitted a Poisson general linear model with the maximum number of territories recorded at each site in each year as the response variable. Site, year (as a continuous variable) and site status (intervention/control) were included as fixed factors along with the proportion of the total area surveyed which consisted of scrub. The latter controlled for the strong influence of scrub area (as a nesting habitat) on the likelihood of territory retention between years (Dunn and Morris 2012). As we were interested in whether site status affected temporal changes in the abundance of territorial doves, we included an interaction between year and status. We analysed both the desired and the actual intervention/control status of study sites (see above; Table S2).

Model selection

In order to identify factors affecting MCP area and breeding success, generalised linear mixed models (GLMMs) were initially used to screen potential predictor variables (Tables 1 and 3) one at a time against the null model containing random effects only. Variables found to be potentially influential (at $P < 0.1$) were tested for multicollinearity, which was found to be weak ($r < 0.5$ in all cases). All potentially influential terms were then included in a global multivariate model, on which we used the ‘dredge’ term in the *MuMIn* library (Barton 2012) to rank all possible model combinations using Akaike’s Information Criteria (AICc) (Burnham and Anderson 2002). Where no single model fitted the data better than any other model (i.e. with no models where Δ AIC was less than 2), we used model averaging on the set of most plausible models (i.e. all with Δ AIC less than 2) to estimate effect sizes (Burnham and Anderson 2002). We interpreted a variable as significantly influencing the response variable where 95% confidence intervals from the averaged model did not overlap zero.

Factors affecting home range size

Our aim was to identify any habitat components that affected home range size. As sampling effort (fix number) commonly influences home range size (e.g. Girard *et al.* 2002), we used a linear mixed-effects model (LMM) (with Gaussian error structure) to describe the form of the relationship between the 90% MCP area (log transformed) and fix number. There was a significant positive linear relationship but no evidence of any non-linearity (quadratic and cubic terms were both non-significant; $P > 0.1$). We therefore screened a set of potential predictors of 90% MCP (described in Table 1) using a null linear mixed-effects model containing nested random terms of nest within bird to account for the non-independence of home ranges of paired doves and of multiple nesting attempts of individual birds, plus fix number as a linear fixed term. As the analysis included home ranges derived solely from incubation stage fixes ($n = 31$), and solely from chick stage fixes ($n = 21$), we included a two-level nest stage factor to test for any differences and included nested random

Table 1. Terms examined as potentially influencing turtle dove home range size. Terms included in a multivariate analysis examining factors influencing home range size, following univariate analyses (which included Fix Number *a priori*), have their variable names italicised.

Variable	Description	Median (range) / levels (<i>n</i>)	Univariate screening	
			L. ratio	<i>P</i>
Nest	ID code for nest: multiple birds for 3 nests and multiple breeding stages for 14 nests	28 nests	Random effect	
Bird	ID code for bird: multiple nests for 10 birds	20 birds	Random effect	
Stage	Breeding stage	Egg (26), Chick (20)	0.434	0.510
<i>Fix Number</i>	Number of fixes for each bird/breeding stage	10 (5–22)	Included <i>a priori</i>	
<i>County</i>	County within which birds were tagged	Essex (24) Norfolk (4)	3.669	0.055
FED	First egg date: back-calculated from known hatch date/ chick age where nest was found during incubation or chick-rearing. 1 = 1 st May	68.5 (22–95)	1.404	0.236
FED ²	See FED		1.792	0.181
<i>Sex</i>	Sex of adult bird	Male (24) Female (22)	3.778	0.052
<i>Year</i>	Year of tagging	2013 (25) 2014 (21)	2.772	0.096
Farm	Farm on which bird was originally radio-tagged	AH (14); HL (3); LI (2); PG (13); SI (1); UH (13)	7.487	0.187
<i>Prop non farmed*</i>	Proportion of non-farmed habitat area within the 90 % MCP. Calculated using rural land registry data, assuming data not on the land registry is not farmed, and excluding urban areas and water	0.27 (0.05–0.99)	8.996	0.003
<i>GA ratio*</i>	Ratio of grass to arable within the 90 % MCP. Calculated as grass area/(grass area + arable area), as assessed by field-collected habitat data	0.11 (0.00–1.00)	2.646	0.104
<i>Prop cereal*</i>	Proportion of predicted 90 % MCP covered by cereal, as assessed by field-collected habitat data	0.40 (0.00–0.98)	0.470	0.493
<i>Prop OSR*</i>	Proportion of predicted 90 % MCP covered by oil seed rape, as assessed by field-collected habitat data	0.05 (0.00–0.69)	0.002	0.962
<i>Seed index*</i>	Scaled weighted seed index (see Table S3) designed to reflect the availability of seed-rich habitat provided through AES	0 (0–1)	6.503	0.011

* denotes habitat terms excluded from the predictive model.

Table 2. Minimal model used to predict home range size for all nests.

Variable	Estimate	SE	t	df	P
Intercept	1.126	0.210	5.36	17	0.001
Fix Number	0.063	0.016	3.88	17	0.002
Sex *	-0.272	0.158	-1.72	17	0.104
County	-0.483	0.276	-1.75	17	0.099

* comparison of the model with and without this term supported its inclusion in the final model (L. ratio₁ = 2.84, P = .09)

Table 3. Terms examined as potentially influencing turtle dove nest survival or nestling biometrics. Median, range (for continuous variables) and levels (for factors) are provided for the whole dataset (each model utilises a subset of the whole dataset). Results of univariate screening for each model are provided in Table 6.

Variable	Description	Median (range) / levels (n)
Bird ID	Bird identifier. Included as a random effect to control for multiple nesting attempts from the same pair.	n = 30 pairs
Nest ID	Nest identification variable. Included in the individual level chick analysis only as a random effect to control for non-independence of nest-mates.	n = 45 nests
County	County within which nest was located	Essex (30 nests); Norfolk (15 nests)
FED	First egg date: back-calculated from known hatch date/ chick age where nest was found during incubation or chick-rearing. 1 = 1 st May	65 (11–116)
FED ²	See FED	
Prop non farmed	Proportion of non-farmed habitat area within the predicted MCP. Calculated using rural land registry data, assuming data not on the land registry is not farmed and excluding urban areas and water.	0.32 (0.05–0.89)
GA ratio	Ratio of grass to arable within the predicted MCP. Calculated as grass area/(grass area + arable area), as assessed by field-collected habitat data	0.14 (0–0.89)
Prop cereal	Proportion of predicted MCP covered by cereal, as assessed by field-collected habitat data	0.31 (0–0.82)
Prop OSR	Proportion of predicted MCP covered by oil seed rape, as assessed by field-collected habitat data	0.01 (0–0.41)
Seed index	Weighted seed index (Table S3) designed to reflect the availability of seed-rich habitat; habitat present in 10 predicted MCPs	0 (0–53.79)
Nest height	Height of nest above ground (m)	2.33 (1.10–4.78)
Nest habitat	Nest site habitat, categorised as either hedgerow (linear feature) or scrub (non-linear feature)	Hedgerow (10 nests); Scrub (35 nests)
Vegetation cover	Nest vegetation cover as assessed by a hemispherical photo placed on the nest facing upwards post-fledging (%)	94.21 (71.55–98.48)
Intervention plot distance	Distance of nest to nearest intervention plot (m)	5321 (97–19,360)
Water distance	Distance of nest to nearest semi-permanent standing water source (pond/lake/reservoir) (m)	72 (1–638)
Human distance	Distance to nearest human habitation, as proxy for distance to artificial food source (m)	83 (25–869)

effects as above. We included two-way interactions between adult sex and FED in multivariate analyses, to test for sex-specific seasonal changes in ranging behaviour.

Prediction of home range size

Tracking data were available for 36 out of 45 nests, from 23 birds. We therefore used a simplified version of the home range LMM (above, but excluding habitat variables as described in the legend to Table 1) to predict 90% MCPs for those nests without tracking data. Assuming a circular home range shape allowed us to derive habitat composition measures from the predicted home range for all nests (with and without tracking data), which could then contribute to analyses of breeding parameters. Terms potentially influential ($P < 0.1$) in univariate analyses (Fix number, County, Year and Sex; Table 1) were included in a multivariate global model. This was simplified using backwards stepwise deletion removing any terms that failed to achieve a conservative significance threshold ($P < 0.1$; Table 2). This model had reasonable predictive power (observed vs. predicted MCP: $r = 0.788$, $P < 0.001$). As the relationship between 90% MCP and fix number showed no clear asymptote, we used the 95th percentile of the available fix number ($n = 17$) to predict 90% MCPs. Female 90% MCPs were 11% larger than those of males (predicted values from the final model of 3.89 ± 0.29 ha for females and 3.49 ± 0.31 ha for males; Table 2), so we predicted areas of the former in order to ensure the inclusion of all potentially important foraging areas. We used these predicted home ranges to define habitat composition around all nests regardless of whether we had actual home range data.

Compositional analysis of foraging habitat selection

To examine foraging habitat preferences of Turtle Doves, we compared usage and availability of intervention plots and other available habitats. AES option availability (for those options included in our seed index; Table S3) was categorised at the field scale according to the presence or absence of AES options within the field, and then further categorised by the crop type within the field. We did this because the exact location of strip options within fields was unknown, and some options (e.g. cultivated fallow, low input spring cereal) are applied at the field scale. The following seven habitat categories were distinguished in the analysis: intervention plots in fields of any crop type (TP); AES in or adjacent to cereal fields (Cereal AES); AES in or adjacent to grassland or other crop fields (Grassland/other crop AES); cereal fields with no AES options (Cereal non-AES); grass fields with no AES options, mostly lightly grazed and ungrazed meadows (Grassland non-AES); other crop fields such as OSR or break crops with no AES options (Other crop non-AES) and apparently unfarmed areas such as amenity land and quarries with no AES options (Non-cultivated non-AES). To calculate foraging habitat, we took the approach described by Dunn *et al.* (2017): briefly, we assumed that each radio-tracking fix of a bird more than 50 m from its nest site was a foraging location and assumed each fix ($n = 529$ foraging locations from 28 birds) to have an accuracy of ± 50 m based on re-sightings and calibrations from nest locations. We calculated the composition of utilised habitat for each bird from a 50 m radius around each foraging location, and the composition of available habitat from a 3-km radius around each nest site (to encompass the mean maximum foraging distance of 2762 m), using the 'gIntersection' command in the *rgeos* package (Bivand *et al.* 2014).

We using the 'compana' function in the *adehabitatHS* package (Calenge 2006) to perform a compositional analysis of habitat use (Aebischer *et al.* 1993). Habitat categories for each bird were expressed as a proportion of the total available or used area, and we then replaced all zero values with 0.0001 because zero values can bias the test as log-ratio differences cannot be computed. We repeated our analysis with additional arbitrary non-zero values (0.001 and 0.00001) because the value selected can potentially influence results. First, we tested whether habitat selection was significant using a Wilk's lambda test, subsequently ranking habitats independently of availability according to the number of differences between each pair of habitat types.

Factors affecting nesting success and nestling biometrics

We tested for any influence of a set of candidate predictors of nesting success and chick biometrics from 45 Turtle Dove nests monitored during 2013 and 2014 (see Table 3). To determine whether nesting success was influenced by habitat composition within the predicted circular 90% MCPs or by the availability of seed-rich habitat, we examined daily nest survival (at the egg and chick stages separately), individual chick survival and the number of fledglings per nesting attempt. We were unable to monitor the nesting activity of enough breeding pairs through the breeding season to estimate the number of breeding attempts per pair per year with confidence. All models contained a pair identifier as a random effect to control for multiple nesting attempts; the individual chick survival model also contained a nest identifier as a random term to control for non-independence of sibling outcomes. GLMMs were used to analyse nest and chick survival, in which the response variable was nest outcome or chick mortality (0 = survived, 1 = failed), with the number of exposure days during the relevant nest stage declared as a binomial denominator (Aebischer 1999, Hazler 2004). For the fledgling GLMM we used the number of fledglings (0–2) within a Poisson error structure.

To test whether nestling mass or condition were affected by home range habitat composition or the availability of seed-rich habitat we constructed two LMMs with Gaussian error structure, designating pair and nest identity as random effects to allow for non-independence of nestlings from the same nest and multiple nests from the same pair. We used residuals from a linear regression of body mass against tarsus length at 7 days old as an index of condition (Labocha and Hayes 2012).

Results

Territory density

The presence of intervention plots on sites ('desired' status) had no influence on the change in Turtle Dove territory abundance over time (Year x desired status interaction: $\chi^2_1=0.084$, $P=0.77$). However, when sites were classified according to the presence of successful intervention plots providing accessible food-rich habitat ('actual' status), those successful intervention sites lost territorial Turtle Doves at a marginally slower rate than sites lacking such successful intervention (Year x actual status interaction: $\chi^2_1=3.202$, $P=0.074$). Sites where accessible seed-rich habitat was successfully provided lost on average 67% of their Turtle Dove territories between 2010 and 2014 compared to a 95% loss on control sites and those with unsuccessful intervention plots (Figure 1).

Factors affecting home range size

Home range size increased linearly with the number of available fixes (Table 4) and decreased with an increasing proportion of non-farmed habitat in the home range (Table 4; Figure 2a). The presence of seed-rich habitat was linearly associated with larger home ranges (Table 4; Figure 2b; quadratic term was non-significant in univariate screening: Likelihood ratio test = 1.69, $P=0.19$).

Foraging habitat selection

Turtle Doves showed significantly non-random selection of foraging habitat types (Wilk's $\lambda=0.16$, $P=0.001$; Table 5; Figure 3), with non-AES grassland the strongest selected habitat, followed by fields containing intervention plots. AES arable and AES grassland/other crop were the least selected habitats (Table 5; Figure 3).

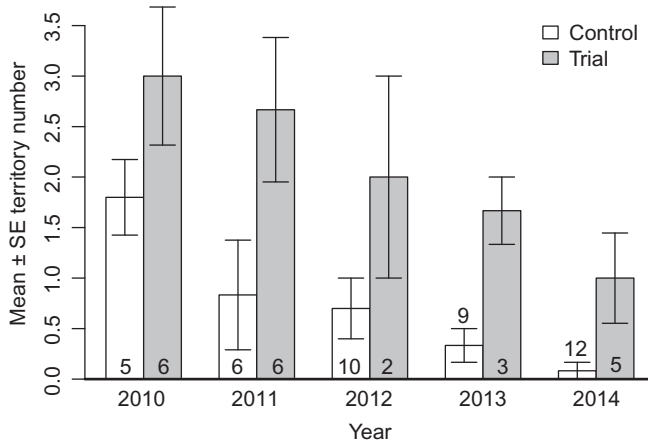


Figure 1. Variation in territory density over time across actual status of study sites with (“trial”) or without (“control”) suitable turtle dove foraging habitat. Sites in 2010 had no intervention but are split into sites forming intervention and control sites during subsequent years for illustration. Bars show raw data ± 1 SE; numbers in or above bars denote sample size of sites.

Table 4. Model averaged results from an LMM analysing terms influencing home range size. Estimates and 95% CIs are model averaged coefficients, and CIs not overlapping zero (bold) are taken to indicate statistical significance.

Variable	No. models	Estimate	SE	Lower CI	Upper CI
Intercept	2	3.150	0.480	2.145	4.156
Fix Number	2	0.127	0.034	0.054	0.200
Prop non farmed	2	-2.134	0.665	-3.580	-0.688
Prop seed	2	1.750	0.652	0.329	3.171
Year	2	-0.507	0.552	-1.827	0.087

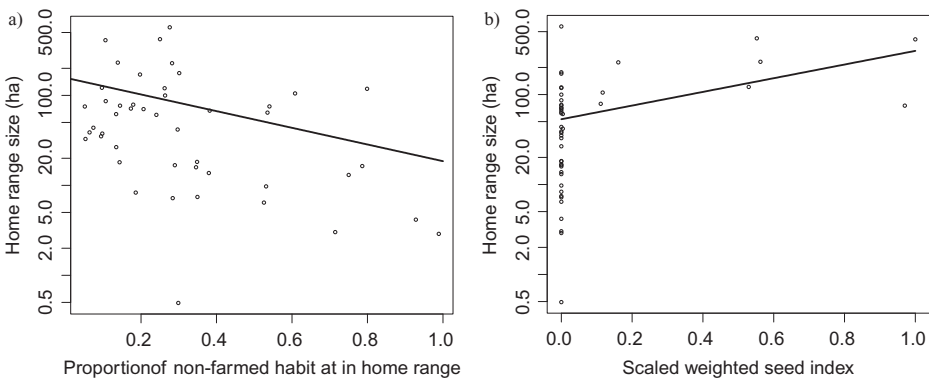


Figure 2. Turtle dove home range size is associated with a) the proportion of non-farmed land and b) the seed index of habitat within the 90% MCP (Table 6). Points display raw data and lines are predicted from the final averaged model (Table 6) with median values of continuous variables (Table 1).

Table 5. Ranking matrix comparing habitat use from foraging locations of breeding turtle doves with available habitat within 3km of the nest ($n = 30$); and b) Selection ratios and confidence intervals for each habitat type.

	TP	Cereal AES	Grassland or other crop AES	Cereal non-AES	Grassland non-AES	Other crop non-AES	Non Cultivated non-AES	Rank
TP	o	+++	+++	+	---	+++	+	5
Cereal AES	---	o	+	---	---	-	---	1
Grassland or other AES	---	-	o	---	---	---	---	0
Cereal non-AES	-	+++	+++	o	---	+	-	3
Grassland non-AES	+++	+++	+++	+++	o	+++	+++	6
Other crop non-AES	---	+	+++	-	---	o	-	2
Non cultivated non-AES	-	+++	+++	+	---	+	o	4

+ indicates a preference for the habitat in the row over the habitat in the column; a triple sign indicates a significant preference ($P < 0.05$). The highest numbered rank (i.e. 6) is the most preferred habitat.

TP: Intervention Plot; AES: Agri-Environment Scheme

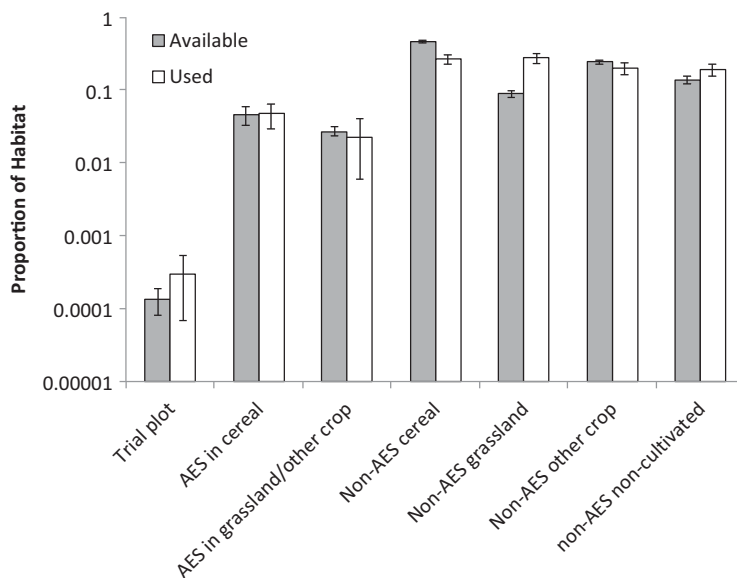


Figure 3. Mean \pm 1 SE proportion of habitat selected by foraging turtle doves ($n=30$) compared to that available within 3km of their nest.

Factors affecting nesting success and chick biometrics

We found no terms influencing whole nest failure at the egg stage (Table 6a), but at the chick stage whole nest failure was higher where home ranges contained more non-farmed habitat (Figure 4a) and a higher ratio of grass to arable (Figure 4b; Table 7a). Individual chick mortality showed a relationship with non-farmed habitat in the same direction and of similar magnitude to that with whole nest failure (Figure 4a; Table 7a). The number of fledglings differed between counties (or clusters), with Essex nests producing more fledglings than nests in Norfolk (Essex: 1.17 ± 0.17 ; Norfolk: 0.38 ± 0.21 fledglings per nest).

Nestling mass at seven days decreased with increasing distance to human habitation (Table 7b; Figure 5). Nestling condition at seven days increased with the proportion of cereal in the home range (Table 6b) and was higher for chicks in scrub nests than for those in hedgerow nests (Figure 6).

Discussion

Conservation interventions that boost food availability have the potential to reverse population declines where food is limiting (e.g. Perkins *et al.* 2011, Baker *et al.* 2012). For the rapidly declining Turtle Dove, changes in abundance of territorial males were marginally less negative on farms where we provided additional accessible seed-rich habitat, and fields containing intervention plots were selected by foraging Turtle Doves. However, neither the availability of seed-rich AES habitat nor the proximity of our intervention plots had any detectable influence on nesting success or nestling biometrics.

Whilst less negative abundance trends on farms with suitable foraging habitat suggest that intervention plots may locally beneficial, overall populations still declined on intervention farms. Turtle Dove population structure and settlement patterns are little studied, but in general, population densities of species tend to become lower closer to their range edge (e.g. Lawton 1993, Holt *et al.* 2005). The UK Turtle Dove population has shown a marked range contraction towards south-east

Table 6. Results of univariate screening for fixed effects potentially influencing a) nest or chick mortality, or b) nestling biometrics. Statistics in bold denote terms included in multivariate analyses. Statistics in italics denote terms excluded from the relevant analysis due to multicollinearity.

a	Egg stage nest		Chick stage nest		Individual chick		Number of fledglings	
	Variable	L. ratio	P	L. ratio	P	L. ratio	P	L. ratio
County	2.619	0.106	1.086	0.297	0.239	0.625	3.430	0.064
Year	0.621	0.431	0.065	0.799	0.481	0.488	0.007	0.935
FED	1.3802	0.240	0.0927	0.761	0.164	0.685	0.507	0.476
FED ²	1.196	0.274	0.619	0.432	0.994	0.319	0.822	0.365
Prop non farmed	1.743	0.187	11.076	<0.001	9.055	0.003	2.341	0.126
GA ratio	1.350	0.245	3.408	0.065	1.291	0.256	2.349	0.125
Prop cereal	1.181	0.277	1.719	0.190	0.138	0.711	1.706	0.192
Prop OSR	0.684	0.408	2.918	0.088	3.637	0.057	0.013	0.908
Seed index	0.108	0.742	1.682	0.195	0.663	0.416	0.799	0.372
Nest height	1.260	0.272	2.772	0.096	1.098	0.295	0.039	0.843
Nest habitat	0.862	0.353	5.996	0.014	5.083	0.024	0.711	0.399
Vegetation cover	0.374	0.541	0.065	0.799	0.009	0.923	0.208	0.648
Intervention plot distance	0.073	0.787	0.033	0.857	0.255	0.613	0.986	0.321
Water distance	0.134	0.715	1.235	0.266	1.830	0.175	0.027	0.871
Human distance	0.034	0.854	0.261	0.609	0.176	0.675	0.034	0.854

b	Mass		Body condition		
	Variable	χ^2	p	L. ratio	P
County		0.199	0.656	5.564	0.018
Year		0.649	0.421	0.069	0.793
FED		0.006	0.939	0.332	0.565
FED ²		0.094	0.759	0.420	0.517
Prop non farmed		0.020	0.888	2.436	0.119
GA ratio		0.775	0.379	1.285	0.257
Prop cereal		1.384	0.240	8.847	0.003
Prop OSR		2.123	0.145	2.403	0.121
Seed index		0.007	0.935	0.210	0.647
Nest height		2.610	0.106	1.775	0.183
Nest habitat		1.722	0.189	5.921	0.015
Vegetation cover		0.664	0.415	0.196	0.658
Intervention plot distance		0.826	0.364	1.621	0.203
Water distance		0.062	0.804	2.774	0.096
Human distance		4.313	0.038	1.396	0.237

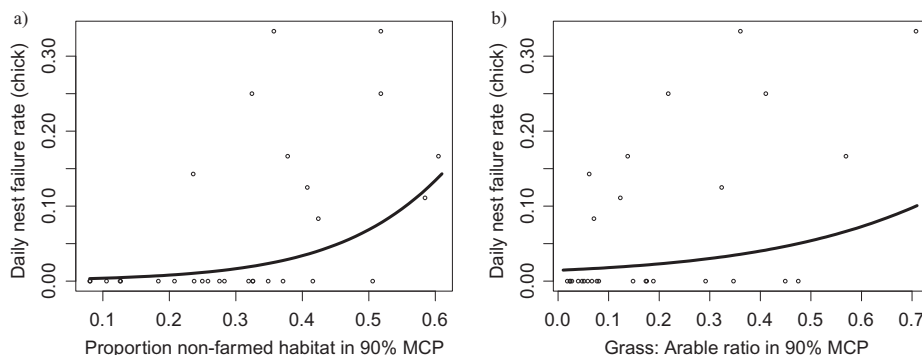


Figure 4. Nest survival at the chick stage was highly correlated with a) the proportion of non-farmed habitat and b) the Grass: Arable ratio within the 90% MCP. Points show raw data; lines are predicted from the final averaged model (Table 7a) with mean scaled nest height (0.48).

England (Gibbons *et al.* 1993, Balmer *et al.* 2013) so our study sites are now nearing the edge of the European breeding range and it seems plausible that abundance may decline faster at range edges due to settlement patterns, rather than habitat effects. The slightly more positive abundance trend on intervention sites suggests a higher probability of settlement at the beginning of the breeding season probably mediated through enhanced habitat quality. Turtle Doves are not thought to be site faithful (Browne and Aebischer 2001) and juveniles may not return to natal breeding areas but settle earlier on the migration route (e.g. Studds *et al.* 2008). A recent range-wide population genetic study of Turtle Dove (Calderón *et al.* 2016) found no evidence of genetic population structure across flyways, suggesting range-wide population admixture.

We could not directly test the effect of our intervention plots on ranging behaviour and reproductive parameters as Turtle Doves dispersed widely following radio-tagging. Only three of the 26 tagged birds for which we had habitat and nesting data had intervention plots within their predicted home ranges and the median distance of a nest to a plot was 5.3 km (range 0.1–19.4 km), although fields containing intervention plots were positively selected by foraging Turtle Doves where available. We therefore constructed a wider 'seed index' which included AES options with the potential to provide suitable seed-rich habitats, although we lacked the resources to undertake direct field assessments of whether these habitats actually provided abundant and accessible seed. However, we did not detect any associations between this predicted availability of seed-rich habitat, and any Turtle Dove reproductive metrics. Thus, our study provides no evidence of any demographic response to the likely availability of seed-rich habitats. The main caveat to this conclusion is that our measure of seed-rich habitat was assumed rather than measured.

The relationship between smaller home ranges and a high proportion of non-farmed habitat within MCPs suggests that unfarmed habitats may represent important foraging habitats allowing birds to occupy smaller home ranges. This is supported by our previous finding of the importance of these habitats for recently fledged Turtle Doves (Dunn *et al.* 2017). Furthermore, our compositional analysis of foraging habitats suggests that extensively managed grassland (non-AES grassland) and unfarmed habitats (non-cultivated non-AES) are selected by foraging Turtle Doves, while fields containing AES options were generally avoided. Further examination of our data indicated that the more utilised foraging habitats consisted of mainly lightly grazed (mostly horse) pastures, semi-natural grassland, amenity land and fallows. Whilst it was beyond the scope of this study to undertake detailed assessment of the habitats present on non-farmed or non-AES land, our observations suggest that many non-farmed habitat patches in our study areas provided more seeding plants, short swards and bare ground than surrounding farmland (Dunn *et al.* 2017). The tendency for relatively large home ranges to contain proportionately little unfarmed habitat, and a

Table 7. Results of multivariate analyses examining a) nest failure and chick mortality, and b) chick biometrics.

a													
Variable	Chick stage nest failure				Individual chick mortality				Fledgling number				
	Est	SE	Lower CI	Upper CI	Est	SE	Lower CI	Upper CI	Est	SE	Lower CI	Upper CI	
Intercept	-5.398	2.058	-9.566	-1.231	-6.228	1.583	-9.390	-3.067	0.154	0.169	-0.239	0.468	
Habitat	*	*	*	*	0.783	1.161	-0.752	4.034	-	-	-	-	
Grass: Arable ratio	2.357	2.205	0.110	7.126	-	-	-	-	-	-	-	-	
Nest height	-2.729	3.534	-12.013	1.193	-	-	-	-	-	-	-	-	
Prop non-farmed	7.411	2.925	1.406	13.417	6.232	2.691	0.827	11.637	-	-	-	-	
Prop OSR	-1.487	5.615	-35.242	11.543	-6.056	8.161	-27.494	5.014	-	-	-	-	
County	-	-	-	-	-	-	-	-	-1.110	0.478	-2.179	-0.264	
b													
Variable	Mass				Body condition								
	Estimate	SE	Lower CI	Upper CI	Estimate	SE	Lower CI	Upper CI					
Intercept	120.813	13.443	90.802	148.565	-22.097	6.635	-35.550	-8.644					
Human distance	-10.451	2.867	-16.363	-3.987	-	-	-	-					
County	-	-	-	-	-2.243	4.608	-18.807	4.528					
Prop cereal	-	-	-	-	41.005	14.353	11.851	70.159					
Habitat (Scrub)	-	-	-	-	11.775	3.245	5.153	18.396					

* term removed from multivariate analysis as its inclusion destabilised the model. Examination of raw data did not suggest an important effect of this variable.

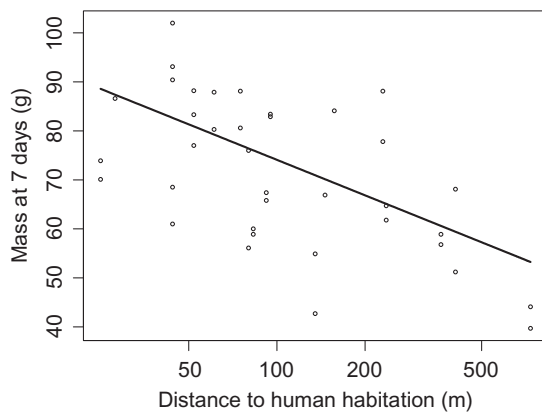


Figure 5. Nestling mass at seven days decreased with increasing distance from human habitation. Points show raw data, line is predicted from the final averaged model (Table 7b) with a mean value for PCA₁ (o); note log x-axis.

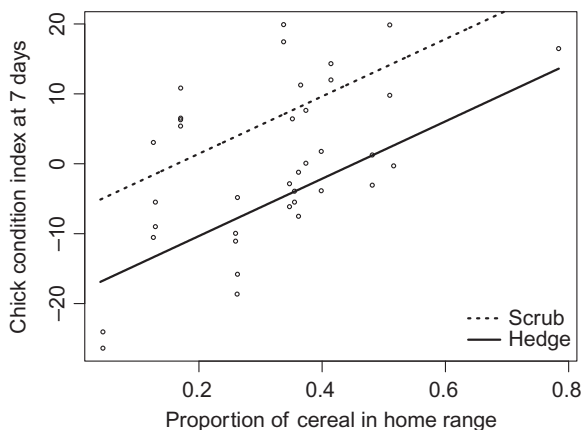


Figure 6. Nestling condition at seven days increased with an increasing proportion of cereal in the home range, and differed between nest habitats. Points show raw data; lines are predicted from the final averaged model (Table 7b) for nests in scrub (solid line) and nests in hedgerows (dotted line) in Norfolk.

high proportion of seed-rich habitat, implies that doves occupying home ranges that lacked unfarmed habitats may have needed to travel further from their nests in order to forage in seed-rich habitats.

Despite the likely greater availability of food in non-farmed habitat, at the chick stage, nest failure was higher where more non-farmed habitat was present within predicted 90% MCPs, with 70% of nest failures at the chick stage ($n = 10$) due to predation. Higher nest failure rates were also associated with a higher ratio of grass to arable land, and gamekeeping in our study areas occurred largely or entirely on arable land. Observations of predators and the examination of depredated nests or nestling remains suggest that mammals were the main nest predators in our study areas (Dunn *et al.* 2017), and the negative impact on chick survival may negate positive impacts of increased food availability on reproductive metrics.

Where nests survived until chicks were seven days old, those nearer human habitation contained significantly heavier chicks. There has been an anecdotal increase in sightings of Turtle Doves foraging under garden bird feeders (BTO GBW, personal communication), supported by molecular analysis of Turtle Dove faecal samples finding a high proportion of Turtle Dove diets to contain sunflower *Helianthus annuus*, *Sorghum* sp., hemp *Cannabis sativa* and niger *Guizotia abyssinica* (Dunn *et al.* 2018), all common components of garden bird seed. This finding suggests that Turtle Doves may be relying on supplementary food sources such as those provided in gardens in order for their chicks to reach adequate weight: elsewhere we show that heavier chicks at seven days old are more likely to survive for 30 days post-fledging (Dunn *et al.* 2017). Supplementary feeding is a widespread practice both in gardens (mainly aimed at passerines, Robb *et al.* 2008), for gamebirds in wider farmland (Sánchez-García *et al.* 2015) and when targeted for conservation objectives (Castro *et al.* 2003, Schoech *et al.* 2007, López-Bao *et al.* 2008, Blanco *et al.* 2011). However, Turtle Doves have a high prevalence of the protozoan parasite *Trichomonas gallinae* (95%: Lennon *et al.* 2013, Thomas 2017), which has been linked to mortality in both adults and nestlings within our study population (Stockdale *et al.* 2015). The *T. gallinae* parasite is spread at shared water and food resources (Stabler 1954); in such instances, supplementary food sources in the form of unmanaged spills from garden bird feeders may be contraindicated as negative impacts may undermine any positive effects (Blanco *et al.* 2011). Recently, new ways of supplementary feeding Turtle Doves without increasing the prevalence of the *T. gallinae* parasite have been tested successfully and rolled out in the Countryside Stewardship AES or as a voluntary measure in England (UK Government 2020).

Nestling body condition was better where a higher proportion of the home range consisted of cereal crops. This contrasts with our previous finding that chicks with a high proportion of cereals in their diet were in poorer body condition (Dunn *et al.* 2018). However, alternative sources of seed food may be available in some arable field margins especially those subject to restricted herbicide application (Vickery *et al.* 2009), which, depending on vegetation structure, may be accessible to foraging Turtle Doves. Before the widespread use of herbicides on arable land, a large proportion of Turtle Dove diet was formed of arable plants such as common fumitory and common chickweed *Stellaria media* (Murton *et al.* 1964), both of which have declined strongly in cereal dominated landscapes over the past 40 years (Potts *et al.* 2010). We previously reported that Turtle Dove nestling condition was positively associated with the proportion of 'natural' (i.e. non-crop, non-supplementary food) items in their diet (Dunn *et al.* 2018).

Conclusions

The abundance of territorial Turtle Doves declined more slowly on sites containing accessible seed-rich intervention plots. Due to the mobility of radio-tagged individuals, we could not directly test effects of our intervention plots on reproductive parameters and our wider seed index may have included areas unsuitable for foraging potentially masking any positive effects of seed-rich areas. Although foraging Turtle Doves selected fields containing intervention plots and may have expanded their home ranges to exploit seed-rich habitats, there was no evidence that the availability of potentially seed-rich habitats influenced breeding success or chick biometrics. Our study highlights the importance of non-farmed habitats (lightly grazed and semi-natural grassland, amenity land, fallows) for breeding Turtle Doves, these being selected by foraging doves and associated with smaller home ranges. However, nest failure rates (mainly linked to predation) were higher in home ranges containing more non-farmed habitats. Future research should focus on linking dietary components to potential habitat sources, and on linking reproductive performance to fine-scale habitat utilisation using recently developed high-resolution tagging technology (e.g. GPS tags). Optimising delivery of various sources of seed to ensure food is abundant, accessible, and does not increase parasite transmission, will be an important conservation challenge for this species. This should be delivered in a variety of ways (i.e. through supplementary feeding, bespoke sown mixtures and encouraging a diversity of natural plants to set seed through enhancement of

existing seed rich, accessible habitats where these are known to already exist) to ensure that seed is available throughout the time that Turtle Doves are present on the breeding grounds, and that the birds have a varied diet. Placing these resources close to suitable nesting habitat and safe water sources will be of most benefit to allow both breeding adults and recently fledged juveniles to obtain all of their key requirements without flying long distances.

Supplementary Materials

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0959270920000635>.

Acknowledgements

This work was funded jointly by the RSPB and Natural England as part of the Action for Birds in England (AfBiE) partnership. Thanks to farmers and landowners in Essex, Suffolk, Norfolk, and Cambridgeshire who sowed intervention plots and allowed access to their land for monitoring nests and radio-tracking birds. Thanks to many staff and volunteers who assisted with radio-tracking and nest monitoring: Jacqui Weir, Kerry Skelhorn, Jenny Bright, Judit Mateos, Eliza Leat, Rebecca Thomas, Alexander Ball, Rebecca Melville, Vivien Hartwell, Joanne Stonehouse, Maureen Gibson, Holly Neville-Smith, Chris Pringle, Rebecca Andrews, Laura Wright, Emma Cutten, Louis O'Neill and Connie Miller. Countryside Stewardship and Environmental Stewardship Options data were provided from Natural England datasets (© Natural England copyright 2014). Thanks to two anonymous reviewers for their comments on an earlier version of the manuscript. Birds were caught and radio-tagged under licence from the British Trust for Ornithology, following approval from the Special Marks Technical Panel.

References

- Aebischer, N. (1999) Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* 46: S22–S31.
- Aebischer, N., Robertson, P. and Kenward, R. (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325.
- Arcece P. and Smith, J. (1988) Effects of population density and supplemental food on reproduction in song sparrows. *J Anim Ecol* 57:119–36.
- Arvidsson, B., Askenmo, C. and Neergaard, R. (1997) Food supply for settling male rock pipits affects territory size. *Anim Behav* 54: 67–72.
- Baker, D., Freeman, S., Grice, P. *et al.* (2012) Landscape-scale responses of birds to agri-environment management: a test of the English Environmental Stewardship scheme. *J. Appl. Ecol.* 49: 871–82.
- Baker, K. (1993) *Identification guide to European non-passerines*. Thetford: British Trust for Ornithology. (BTO Guide 24).
- Balmer, D., Gillings, S., Caffrey, B., *et al.* (2013) *Bird atlas 2007–11*. Thetford, UK: British Trust for Ornithology.
- Barton, K. (2012) MuMIn: Multi-model inference. R package version 1.7.7. <http://CRAN.R-project.org/package=MumIn>.
- Bivand, R., Rundel, C., Pebesma, E., *et al.* (2014) Package 'rgeos'. <http://cran.r-project.org/web/packages/rgeos/rgeos.pdf>
- Blanco, G., Lemus, J. and García-Montijano, M. (2011) When conservation management becomes contraindicated: impact of food supplementation on health of endangered wildlife. *Ecol. Appl.* 21: 2469–2477.
- Boatman, N., Brickle, N., Hart, J., *et al.* (2004) Evidence for the indirect effects of pesticides on farmland birds. *Ibis* 146: 131–143.
- Bright, J., Morris, A., Field, R., *et al.* (2015) Higher-tier agri-environment scheme enhances breeding densities of some priority farmland birds in England. *Agric. Ecosyst. Environ.* 203: 69–79.

- Browne, S. and Aebischer, N. (2001) *The role of agricultural intensification in the decline of the Turtle Dove* *Streptopelia turtur*. Peterborough: English Nature.
- Browne, S. and Aebischer, N. (2003) Habitat use, foraging ecology and diet of Turtle Doves *Streptopelia turtur* in Britain. *Ibis* 145: 572–582.
- Browne, S. and Aebischer, N. (2004) Temporal changes in the breeding ecology of European Turtle Doves *Streptopelia turtur* in Britain, and implications for conservation. *Ibis* 146: 125–137.
- Burnham, K. and Anderson, D. (2002) *Model selection and multi-model inference: A practical information-theoretic approach*. 2nd edition. New York: Springer-Verlag.
- Calderón, L., Campagna, L., Wilke, T., et al. (2016) Genome-wide evidence of demographic fluctuations and lack of genetic structure across flyways in a long distance migrant, the European turtle dove. *BMC Evol. Biol.* 16: 37.
- Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* 197: 516–519.
- Calladine, J., Buner, F. and Aebischer, N. (1999) Temporal variations in the singing activity and the detection of Turtle Doves *Streptopelia turtur*: implications for surveys. *Bird Study* 46: 74–80.
- Castro, I., Brunton, D., Mason, K., et al. (2003) Life history traits and food supplementation affect productivity in a translocated population of the endangered Hihi (*Stitchbird*, *Notiomystis cincta*). *Biol. Conserv.* 114: 271–280.
- Dunn, J. and Morris, A. (2012) Which features of UK farmland are important in retaining territories of the rapidly declining Turtle Dove *Streptopelia turtur*? *Bird Study* 59: 394–402.
- Dunn, J., Morris, A. and Grice, P. (2015) Testing bespoke management of foraging habitat for European turtle doves *Streptopelia turtur*. *J. Nat. Conserv.* 25: 23–34.
- Dunn, J., Morris, A. and Grice, P. (2017) Post-fledging habitat selection in a rapidly declining farmland bird, the European Turtle Dove *Streptopelia turtur*. *Bird Conserv. Internatn.* 27: 45–57.
- Dunn, J., Stockdale, J., Moorhouse-Gann, R., et al. (2018) The decline of the Turtle Dove: Dietary associations with body condition and competition with other columbids analysed using high-throughput sequencing. *Mol. Ecol.* 27: 3386–3407.
- Frazer, G. W., Canham, C. and Lertzman, K. (1999) *Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation*. Burnaby, British Columbia and Millbrook, New York: Simon Fraser University and the Institute of Ecosystem Studies.
- Gibbons, D., Reid, J. and Chapman, R. (1993) *The new atlas of breeding birds in Britain and Ireland: 1988–1991*. London, UK: T & AD Poyser.
- Girard, I., Ouellet, J-P., Courtois, R., et al. (2002) Effects of sampling effort based on GPS telemetry on home-range size estimations. *J. Wildl. Manage.* 66: 1290–1300.
- Harrison, T., Smith, J., Martin, G., et al. (2010) Does food supplementation really enhance productivity of breeding birds? *Oecologia* 164: 311–320.
- Hart, J., Milsom, T., Fisher, G., et al. (2006) The relationship between yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. *J. Appl. Ecol.* 43: 81–91.
- Hazler, K. (2004) Mayfield logistic regression: A practical approach for analysis of nest survival. *Auk* 121: 707–716.
- Holt, R., Keitt, T., Lewis, M., et al. (2005) Theoretical models of species' borders: single species approaches. *Oikos* 108: 18–27.
- Labocha, M. and Hayes, J. (2012) Morphometric indices of body condition in birds: A review. *J. Ornithol.* 153: 1–22.
- Lack, D. (1954) *The natural regulation of animal numbers*. Oxford, UK: Clarendon Press.
- Lawton, J. (1993) Range, population abundance and conservation. *Trends Ecol. Evol.* 8: 409–413.
- Lennon, R., Dunn, J., Stockdale, J., et al. (2013) Trichomonad parasite infection in four species of Columbidae in the UK. *Parasitology* 140: 1368–1376.
- López-Bao, J., Rodríguez, A. and Palomares, F. (2008) Behavioural response of a trophic

- specialist, the Iberian lynx, to supplementary food: Patterns of food use and implications for conservation. *Biol. Conserv.* 141: 1857–1867.
- Martin, T. (1987) Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Syst.* 18: 453–487.
- Murton, R., Westwood, N. and Isaacson, A. (1964) The feeding habits of the Woodpigeon *Columba palumbus*, Stock Dove *C. oenas* and Turtle Dove *Streptopelia turtur*. *Ibis* 106: 174–188.
- Natural England (2012a) *Entry Level Stewardship: Environmental stewardship handbook. Fourth Edition - January 2013*. Peterborough: Natural England.
- Natural England (2012b) *Higher Level Stewardship. Environmental stewardship handbook. Third Edition*. Peterborough: Natural England.
- PECBMS (2019) *Population trends of common European breeding birds: 2018 update*. Prague: Pan-European Common Bird Monitoring Scheme.
- Perkins, A., Maggs, H., Watson, A., et al. (2011) Adaptive management and targeting of agri-environment schemes does benefit biodiversity: a case study of the corn bunting, *Emberiza calandra* J. *Appl. Ecol.* 48: 514–522.
- Plummer, K., Bearhop, S., Leech, D., et al. (2013) Winter food provisioning reduces future breeding performance in a wild bird. *Sci. Rep.* 3: 2002.
- Potts, G., Ewald, J. and Aebischer, N. (2010) Long-term changes in the flora of the cereal ecosystem on the Sussex Downs, England, focusing on the years 1968–2005. *J. Appl. Ecol.* 47: 215–226.
- R Core Team (2016) *R: A language and environment for statistical computing*.
- Redfern, C. and Clark, J. (2001) *Ringers' manual*. Thetford, UK: British Trust for Ornithology.
- Robb, G., McDonald, R., Chamberlain, D., et al. (2008) Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* 6: 476–484.
- Ruffino, L., Salo, P., Koivisto, E., et al. (2014) Reproductive responses of birds to experimental food supplementation: a meta-analysis. *Front. Zool.* 11: 80.
- Sánchez-García, C., Buner, F. and Aebischer, N. (2015) Supplementary winter food for gamebirds through feeders: Which species actually benefit? *J. Wildl. Manage.* 79: 832–845.
- Schoech, S., Bridge, E., Boughton, R., et al. (2007) Food supplementation: A tool to increase reproductive output? A case study in the threatened Florida Scrub-Jay. *Biol. Conserv.* 141: 162–173.
- Stabler, R. (1954) *Trichomonas gallinae*: A review. *Exp. Parasitol.* 3: 368–402.
- Stockdale, J., Dunn, J., Goodman, S., et al. (2015) The protozoan parasite *Trichomonas gallinae* causes adult and nestling mortality in a declining population of European Turtle Doves, *Streptopelia turtur*. *Parasitology* 142: 490–498.
- Studds, C., Kyser, T. and Marra, P. (2008) Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proc. Natl. Acad. Sci.* 105: 2929–2933.
- Thomas, R. (2017) Molecular epidemiology of *Trichomonas gallinae* in Turtle doves (*Streptopelia turtur*). PhD thesis. University of Leeds, UK.
- Tollington, S., Greenwood, A., Jones, C., et al. (2015) Detailed monitoring of a small but recovering population reveals sublethal effects of disease and unexpected interactions with supplemental feeding. *J. Anim. Ecol.* 84: 969–977.
- UK Government (2020) Countryside Stewardship Scheme. SP9: Threatened Species Supplement. [https://www.gov.uk/countryside-stewardship-grants/threatened-species-supplement-spo#Turtle Dove](https://www.gov.uk/countryside-stewardship-grants/threatened-species-supplement-spo#Turtle%20Dove), accessed 2020-04-20.
- Vickery, J. A., Feber, R. E. and Fuller, R. (2009) Arable field margins managed for biodiversity conservation: a review of food resource provision for farmland birds. *Agric. Ecosyst. Environ.* 133: 1–13.