Commentary

How can functional space for farmland birds best be studied? A comment on Butler and Norris (2013)

A B S T R A C T

Butler and Norris (2013) describe a modelling framework designed to predict farmland bird population trends with reference to the resources provided by the habitats found at the sites. There are several important problems with the approach taken by Butler and Norris and with its suitability for the specific data to which it is applied. Principally, these are over-simplistic conceptual assumptions about habitat effects on abundance, analytical inefficiencies, a failure to consider stochasticity in annual survey data and an absence of evidence linking habitat information recorded in the field to true resource provision.

Modelling frameworks can be valuable alternatives to expensive field data collection for predicting the effects of environmental change and sound new initiatives in this field would be welcome.

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1. Introduction

The concept of functional space (FS), i.e. quantities of critical resources provided by different components of local habitat, is potentially very powerful and useful as a means of facilitating the identification of critical habitat relationships for different taxa. Such relationships would be independent of geographical location, local land-use and vegetation communities. They would allow the construction of generalized models that are applicable across different habitats, landscapes or bioclimatic zones (e.g. Fahrig et al., 2011) and thus provide efficient, mechanistic approach to determining impacts of land-use. This would also represent a novel approach to considering the determinants of the distribution and abundance of species that show varying preferences in terms of apparent habitat use across their ranges (Whittingham et al., 2007; Fuller, 2012). In these respects, the recent paper by Butler and Norris (2013) is welcome, but there are significant problems with their interpretation of the FS concept and with the analyses they present. Consequently, the results that do not simply re-iterate those of previous analyses of the same data sets, such as the dependence of granivorous bird population trends on winter stubble area (Gillings et al., 2005), seem more consistent with a random pattern resulting from the combination of large, spatially complex data sets than with new or biologically meaningful insights. It is important that the correct conclusions are drawn from Butler and Norris' results about how possible dependence on FS should be modelled and about how extensive survey data sets can be used in this context. In particular, it is critical that misleading messages are not understood about the relative utility of a derived model versus empirical data for understanding the effects of changes in management on biodiversity.

Butler and Norris (2013) presented an analysis of BTO/JNCC/RSPB Breeding Bird Survey (BBS) farmland bird data from 1994 to 2007 with respect to habitat information recorded within the same scheme and winter habitat recorded during 1999–2003 under the BTO Winter Farmland Bird Survey (WFBS). The BBS is a UK-wide, annual, volunteer survey, in which observers visit the same 1 km survey square twice each year, walking the same two 1 km transects on each visit and counting all birds seen and heard on each visit. Maximum total counts per visit are commonly used as the final count for each square. Observers record bird and habitat data in 200 m sections of transect, the latter data using a standard scheme of habitat codes (Crick, 1992). The data are analyzed annually to inform about national and regional bird population trends (Baillie et al., 2012) and periodically to address other issues, such as patterns of change in diversity (Davey et al., 2012), influences of habitat on abundance (Siriwardena et al., 2012), relative importance of habitat and weather in driving population change (Eglington and Pearce-Higgins, 2012) and effects of agri-environment management on population growth rates (Baker et al., 2012).

Butler and Norris (2013) estimated 1 km-square-specific log-linear population trends over the period 1994–2007 for 19 species. They also considered all BBS habitat categories and designated each as providing high quality, low quality or zero resources for winter food, breeding season food and/or nest sites for each species. How this process was conducted was not described, but these were considered to encompass all resources required by each species. Scores derived from the total number of 200 m transect sections in which habitat designated as providing each resource were summed as indices of the total species-specific FS in each 1 km square. The square-specific linear population trend estimates were then used

as species-specific dependent variables in models with FS scores as predictors for each species. Spatial autocorrelation is generally low between BBS squares, because they are generally well spaced in the landscape and broad habitat coverage is heterogeneous at the scale of 1 km squares, but Butler and Norris (2013) chose to incorporate a term describing average abundance in the landscape in their models. This term, "LANDABUND", consisted of average abundance of the species concerned across all other BS squares in the data set, weighted by the inverse of the distance from the focal square. Model selection using information criteria and confidence intervals around parameter estimates were the only diagnostics used by Butler and Norris (2013) to assess model quality. The results showed a combination of positive, negative and (mostly) non-significant associations between population trends and both FS and LANDABUND across species. Positive FS results were interpreted as showing beneficial effects of resource availability for population growth and negative results as possible evidence for ecological traps, while interactions with LANDABUND were interpreted as showing the influences of population context, despite the large size of inter-square distances relative to the home ranges of most of the species considered.

2. Measuring functional space

Butler and Norris (2013) divide the FS required by birds into three categories, namely diet (meaning food availability), foraging habitat and nest sites. While models necessarily simplify reality, this represents a gross simplification, for example ignoring the importance of vegetation structures for roosting or predator avoidance. Even accepting this, there are two critical problems with the rest of the process for defining FS from these categories. First, they are considered only as breeding cover, summer foraging cover and winter foraging cover. Hence, food availability and foraging cover are conflated; they are also only identified by gross habitat type. In reality, there is often enormous variability in food availability and/or accessibility between superficially similar habitats (e.g. crop stubbles and grassland: Atkinson et al., 2005; Butler et al., 2005; Robinson and Sutherland, 1999). The separation into high and low quality habitat categories is a further over-simplification of reality, because habitat quality actually often varies considerably along multiple interacting gradients (Fuller, 2012). Second, and more fundamentally, the conceptual assumption with considering three axes of FS is that all are, simultaneously, potentially important determinants of presence or abundance. It is true, assuming that resource requirements are characterized accurately, that all must be present within a viable annual home range for a focal species to be present. However, this qualitative rule does not necessarily translate into a quantitative one that would then allow prediction of variation in abundance, especially when winter ranges are likely to be considerably larger than breeding ones. In practice, one resource is likely to limit populations in any given space and time, so it is variation in that resource that will predict abundance and variation in other resources may have little effect (see, e.g., Robinson et al., 2001). This should be considered when interpreting the results of the tests of FS variables. Moreover, in an environment like farmland, where land-use and management are broadly consistent over large areas, the same resource limitation probably usually applies across extensive areas of land. Such a pattern almost certainly underlies the patterns of population change seen in British granivorous farmland birds since the 1960s (e.g. Siriwardena et al., 2000, 2007), notwithstanding some evidence that different demographic drivers might affect the same species in widely separated, isolated populations (Wilson et al., 2007). Further, it is likely that non-limiting environmental resources become increasingly abundant as species decline because competition is reduced. Most of the

species considered by Butler and Norris (2013) have been in long-term decline (Baillie et al., 2012), therefore weakening the validity of their FS definitions further. It is difficult to make conclusions about relationships with FS variables when population-limiting habitat components are unknown.

If the concepts applied by Butler and Norris are accepted, it is then critical that FS is actually measured accurately. However, they provide no validation or justification for the allocation of BBS and WFBS codes to FS categories, or of the methods by which the codes were translated into quantitative habitat areas. For example, it is not described how qualitative data for linear features in 200 m transect sections were converted to areas of breeding habitat. These habitat data are limited by what can practically be collected by volunteers in the field and data on linear features are focused on the habitats along survey transect routes, which are unlikely to be a random selection of the linear features in a 1 km square. Importantly, the data do not include many key habitat features that determine habitat quality and food availability, and that, in turn, are likely to be critical in determining the real suitability of cover types for breeding and feeding. Such features include sward structure (Atkinson et al., 2005; Buckingham et al., 2006; Perkins et al., 2000), the structural heterogeneity of vegetation (Douglas et al., 2009) and the longevity of stubble fields into late winter (Siriwardena et al., 2008). The absence of such subtle features limits the utility of these data to delimit FS, let alone high and low quality resource provision, except where gross habitat forms a good proxy for resource availability. Such a proxy effect probably underlies the findings of a previous analysis of the data used by Butler and Norris (2013) (Gillings et al., 2005). In this case, total stubble area was probably correlated with high quality and/or late winter stubble simply because they are more likely to occur, on average, where stubble is more common. Butler and Norris (2013) declare that "sufficient data were available to confidently define the contributions of all cover types recorded in BBS and WFBS to FS" for all but one species, but no evidence is provided to support this statement and even a cursory glance at Table S1 reveals clear anomalies, such as unenclosed grass moor representing "high quality breeding habitat" for corn bunting.

3. Data issues

It should also be noted that both BBS and WFBS are sample surveys, designed to inform about large-scale patterns by averaging low-sampling effort local data at the landscape scale. The methods are not appropriate for investigating inter-annual patterns at the scale of the 1 km survey square, because visit-specific bird counts are highly stochastic, only two visits are conducted each year and the habitat data are coarse and focused around the survey transects, rather than describing the square as a whole. Hence, successful analyses of these data have focused on average patterns across whole landscapes (e.g. Gillings et al., 2005; Baker et al., 2012). Square-specific analyses can be valuable, given appropriate statistical methods and interpretation to account for the inherent uncertainty, but the latter has the potential to generate significant noise in assessments of relationships with FS. Accurate data on local populations are best gathered through multiple visits, using territory mapping, while matching habitat data to inform about FS would best be collected across the whole survey area.

4. Analytical methods

Butler and Norris (2013) apply a two-stage analytical process, in which population trends are calculated first at the site-level, i.e. attempting to define site-scale processes. Even if the validity of estimating site-level population trends from BBS data is accepted, this