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Contributed Paper

Bird conservation and the land sharing-sparing continuum in farmland-dominated landscapes of lowland England

Tom Finch,[1,2]* Simon Gillings,[3] Rhys E. Green,[1,2] Dario Massimino,[3] Will J. Peach,[1] and Andrew Balmford[2]

[1]RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire, U.K.
[2]Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, U.K.
[3]British Trust for Ornithology, Thetford, Norfolk, U.K.

Abstract: Empirical evidence from many regions suggests that most species would be least negatively affected if human food demand were met through high-yield agricultural production and conservation of nonfarm ecosystems (land sparing), rather than through wildlife-friendly farming over a larger area (land sharing). However, repeated glaciation and a long history of agriculture may lead to different results in regions such as western Europe. We compared the consequences of land sparing and land sharing on breeding bird species in 2 lowland regions of England, The Fens, with 101 species, and Salisbury Plain, with 83. We derived density–yield responses for each species and then estimated regional population size under regional food production strategies, including land sharing and land sparing, a range of intermediate strategies, and a novel mixed strategy. In both regions, more species achieved maximum regional population size under land sparing than land sharing. In The Fens, the majority of birds were loser species (estimated to have smaller populations under all food production strategies than in the preagricultural baseline scenario), whereas in Salisbury Plain the majority were winners (smaller populations in the preagricultural baseline scenario). Loser species overwhelmingly achieved maximum regional population size under land sparing, whereas winner species achieved maximum regional population size under either land sharing or an intermediate strategy, highlighting the importance of defining which groups of species are the target of conservation. A novel 3-compartment strategy (combining high-yield farming, natural habitat, and low-yield farming) often performed better than either land sharing or land sparing. Our results support intermediate or 3-compartment land-sparing strategies to maximize bird populations across lowland agricultural landscapes. To deliver conservation outcomes, any shift toward land sparing must, however, ensure yield increases are sustainable in the long term, do not entail increased negative effects on surrounding areas, and are linked to allocation of land for nature.

Keywords: agriculture, conservation, land sharing, land sparing, temperate birds, wildlife-friendly farming

Conservación de Aves y el Continuo de Suelo Compartido-Reservado en Paisajes Dominados por Tierras de Cultivo en las Tierras Bajas de Inglaterra

Resumen: La evidencia empírica proveniente de muchas regiones sugiere que la mayoría de las especies se verían menos afectadas negativamente si se cumpliera con la demanda humana de alimentos por medio de una producción agrícola de alto rendimiento y la conservación de ecosistemas no agrícolas (dosificación de suelo) en lugar de hacerlo a través de la agricultura amigable con la fauna en un área mayor (partición de suelo). Sin embargo, la glaciación repetitiva y una larga historia agrícola podrían brindar diferentes resultados en regiones como Europa occidental. Comparamos las consecuencias de la dosificación y la partición de suelo sobre especies de aves en reproducción en dos regiones de tierras bajas en Inglaterra: Los Fens, con 101 especies, y la Planicie Salisbury, con 83 especies. Derivamos las respuestas con densidad de rendimiento para cada especie y después

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*email tom.finch21@gmail.com

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estimamos el tamaño poblacional regional bajo estrategias regionales de producción de alimentos, incluyendo la dosificación y la partición de suelo, una gama de estrategias intermedias y una novedosa estrategia mixta. En ambas regiones, más especies alcanzaron el tamaño poblacional máximo para la región bajo la dosificación del suelo que bajo la partición del suelo. En Los Fens, la mayoría de las aves fueron especies perdedoras (se estimó que tendrían tamaños poblacionales menores bajo todas las estrategias de producción de alimento que en el escenario pre-agrícola de la línea base) mientras que en la Planicie Salisbury, la mayoría de las especies fueron ganadoras (con poblaciones más pequeñas en el escenario pre-agrícola de la línea base). Las especies perdedoras tuvieron abrumadoramente un tamaño poblacional máximo para la región bajo la dosificación de suelo, mientras que las especies ganadoras tuvieron este máximo poblacional bajo la partición de suelo o alguna estrategia intermedia, lo que resalta la importancia de la definición de cuáles grupos de especies son el objetivo de conservación. Una estrategia novedosa de tres compartimentos (combina la agricultura de alto rendimiento, el hábitat natural y la agricultura de bajo rendimiento) muchas veces tuvo un mejor desempeño que la dosificación o la partición del suelo. Nuestros resultados respaldan a las estrategias de dosificación de suelo intermedias o de tres compartimentos para maximizar las poblaciones de aves en todos los paisajes agrícolas de las tierras bajas. Para brindar resultados de conservación, cualquier cambio hacia la dosificación del suelo, sin embargo, debe asegurar que los incrementos en el rendimiento son sustentables a largo plazo, no conllevan un incremento de efectos negativos en las áreas circundantes, y que están vinculados a la asignación de suelo para la naturaleza.

Palabras Clave: agricultura, agricultura amigable con la fauna, aves de clima templado, conservación, dosificación de suelo, partición de suelo

摘要: 来自许多地区的经验证据表明, 如果人类通过高产农业和保护非农业生态系统的方式 (土地分离) 来满足粮食需求, 而不是通过在较大范围内开展野生动物友好型农业 (土地共享), 那么大多数物种受到的负面影响会是最小的。然而, 一些地区 (如西欧) 经历过多次冰川作用, 且有着悠久的农业历史, 可能在这个问题上有所不同。我们比较了英国两个低地地区土地分离和土地共享对繁殖鸟类的影响, 其中东部沼泽地区 (The Fens) 有 101 种鸟, 索尔斯堡平原 (Salisbury Plain) 有 83 种鸟。我们估计了每个物种的密度-产量响应关系, 并评估了各种区域粮食生产策略下鸟类的区域种群大小, 这些策略包括土地分离、土地共享、一系列中间型策略以及一种新型混合策略。在这两个地区, 较多物种在土地分离策略 (而不是土地共享策略) 下的区域种群大小最大。在沼泽地区, 大部分鸟类物种属于失败者 (据估计, 它们在任何粮食生产策略下的种群数量都低于未发展农业时的基线水平); 而索尔斯堡平原的大多数鸟类物种都是成功者 (未发展农业时的基线水平更低) 。失败物种绝大多数都在土地分离策略下可以达到最大区域种群数量, 而成功物种则会在土地共享或中间型策略下达到最大区域种群数量。这一结果突显了确定保护目标中鸟类类型的重要性。此外, 还存在一种新型的三区分隔策略 (结合了高产农业、自然生境和低产农业), 它的效果往往比单一的土地分离或土地共享更好。我们的结果支持选择中间型或三区分隔型土地分离策略, 以求在低地农业景观中使鸟类种群数量最大化。然而, 要取得保护成效, 还应确保在向土地分离策略的转型中, 产量的增长可长期持续、不会为周围地区带来更多负面影响, 且与自然用地的分配相关联。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 农业, 保护, 土地分离, 土地共享, 野生动物友好型农业, 温带鸟类

Introduction

Agriculture is the leading threat to biodiversity globally (Green et al. 2005; Tilman et al. 2017). It drives the destruction of natural habitats (Fehlenberg et al. 2017), and the intensive management of existing agricultural land has negative consequences for many species (Eglington & Pearce-Higgins 2012). These twin threats have motivated 2 contrasting strategies for reconciling food production and nature conservation. Land sharing aims to mitigate the effects of intensification by promoting wildlife-friendly farming. When these interventions reduce yield (production per unit area), more farmland is required to achieve a given amount of food production. In contrast, land sparing involves maximizing farmland yield so that substantial areas of land (>1 km^2 units) can be protected or restored as natural habitat (Balmford et al. 2015). A continuum of intermediate strategies falls between extreme sharing (farming at the minimum yield capable of meeting demand with no spared land) and sparing (meeting demand at the highest possible yield and sparing all remaining land for conservation). Although land sharing and land sparing are typically viewed as mutually exclusive, mixed strategies incorporating features of both (e.g., high-yield farmland alongside wildlife-friendly farmland and natural or seminatural areas) are also conceivable, though rarely assessed (Butsic & Kuemmerle 2013; Law et al. 2016) (Fig. 1).

The consequences of these contrasting strategies for regional species population sizes can be evaluated based on relationships between each species population density and agricultural yield (Green et al. 2005). Empirical studies of this kind conclude that a majority of species would be favored by land sparing (e.g., Phalan et al. 2011; Kamp et al. 2015; Williams et al. 2017), but many derive from the tropics, and none consider mixed strategies.

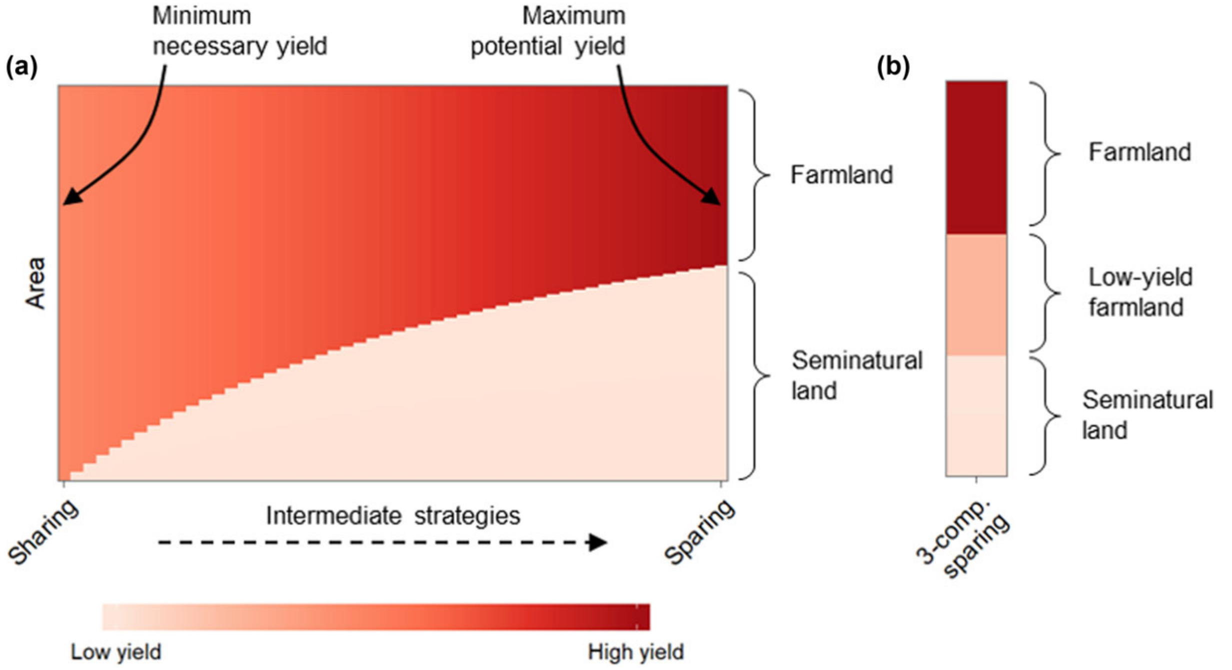

Figure 1. Food production strategies: (a) continuum of 2-compartment strategies (from land sharing to land sparing, where the 2 compartments are farmed land and seminatural (spared) land, with farmland yield and seminatural area increasing from sharing [left] to sparing [right]) and (b) 3-compartment land-sparing strategy containing an additional land-use compartment (low-yield farmland). Each strategy (represented by a vertical column) achieves the same fixed food production target and has the same total area (represented by column height). Seminatural habitat is not necessarily 0 yielding; in our examples, small amounts of meat are produced as a byproduct of conservation grazing.

Europe, in contrast to the tropics, has long been subject to disturbance by glaciations and agriculture. The resulting extinction of species dependent on natural areas (Balmford 1996) might result in proportionally fewer extant species benefitting from land sparing compared with previously studied regions (Ramankutty & Rhemtulla 2012). Even if land sparing maximizes the population of most species, it may cause further declines among culturally valued farmland-dependent species (Eaton et al. 2015; Lamb et al. 2019). Mixed strategies that promote wildlife-friendly farming alongside spared natural habitat may therefore be particularly relevant here.

A further consideration is the nature of spared land, which may alter the response of species to the land sharing-sparing continuum (Macchi et al. 2016). In the United Kingdom, the absence of large tracts of natural areas means that the pre-agricultural natural baseline is contested (e.g., Alexander et al. 2018), and the type of seminatural land cover in any location is determined by management (e.g., presence and density of grazing semiferal livestock).

For 2 contrasting regions of lowland England currently dominated by agriculture, we derived density–yield responses for all assessable bird species and used them to estimate population sizes under a range of regional food production strategies. These include the land sharing-sparing continuum (Fig. 1a) and a 3-compartment land-sparing scenario, a novel mixed strategy in which high-yield farming spares land for both low-yield farmland and seminatural area (Fig. 1b). We also considered scenarios with different ratios of alternative seminatural land covers on spared land. Our expectation was that species with smaller populations now than before the advent of agriculture (losers) (Phalan et al. 2011) will, in aggregate, benefit from the habitat restoration associated with sparing, whereas species with larger populations in the presence of agriculture (winners) will be favored by strategies closer to land sharing. To our knowledge, we are the first to address these questions in the intense agricultural landscapes typical of western Europe.

Methods

Study Regions

We focused on 2 contrasting National Character Areas (NCAs) in the English lowlands (Supporting Information). The Fens is a drained wetland now dominated by large-scale cultivation of arable and horticultural crops. The small areas of remaining natural and seminatural areas can be broadly characterized as either fen (a mosaic of *Phragmites* reed swamp, wet woodland, and open water) or seasonally flooded neutral grassland. The loss of peat on drained land represents a major environmental concern (Natural England 2015*a*). Salisbury Plain and West Wiltshire Downs (Salisbury Plain) is characterized by rolling mixed farmland dominated by cereals and grazing livestock, and several large areas of chalk grassland (with small patches of mixed scrub) and smaller patches of broadleaf woodland. Diffuse pollution (from agriculture) of freshwater habitats and drinking water supplies is of significant concern (Natural England 2015*b*).

Each study region was defined by the Ordnance Survey 1-km grid squares within each NCA. To ensure that all focal squares were environmentally comparable, we used NATMAP Soilscape definitions (Farewell et al. 2011) to exclude squares with <50% cover of peaty soil (raised bog peat soils, fen peat soils, or soils with a peaty surface) in The Fens or limey soil (freely draining lime-rich loamy soils or shallow lime-rich soils over chalk or limestone) in Salisbury Plain. This left 1,228 squares in The Fens (after excluding 2 small, isolated areas ~40 km to the north) and 1,026 in Salisbury Plain.

To estimate the land-use composition of each square we used the Centre for Ecology & Hydrology (CEH) Land Cover plus: crops where possible and the less specific CEH Land Cover Map 2015 (LCM) (Rowland et al. 2017) for parcels with no crop data (Supporting Information). Next, we identified areas currently spared as large (>1 km^2) blocks of natural or seminatural land (Supporting Information). In The Fens, where spared land is scarce and largely restricted to nature reserves, we identified all reserves >1 km^2 ($n = 7$; total area = 43.4 km^2; range = 1.5–20.2 km^2). In Salisbury Plain, where there is more spared land, we identified all contiguous patches of natural and seminatural land covers (calcareous grassland, woodland, or inland rock) >1 km^2 ($n = 12$; total area = 257.2 km^2; range = 1.1–92.1 km^2). We then classified each spared patch, according to the dominant land cover as either fen or wet grassland in The Fens and chalk grassland or woodland in Salisbury Plain.

To transform these spared patches to the regular 1-km grid (so treating all 1-km squares as either spared or farmed), we identified all 1-km squares overlapped by each spared patch and then classified overlapping 1-km squares as spared in descending order of overlap area until the total number of selected squares matched the total area of each patch (rounded to the nearest 1 km^2). Finally, we applied the land-use composition within each spared patch to each corresponding spared square (illustrated in Supporting Information).

Estimating Breeding Bird Densities

We identified all species with potential breeding populations in each region with the Bird Atlas 2007–11 (Balmer et al. 2013). We excluded aerial foragers, nocturnal species, introduced species, and gulls and terns (Supporting Information). For most species, we then used Breeding Bird Survey data (BBS) (described below) to estimate their density in farmland (of varying yield) and on natural and seminatural land. For some rarer species and for wet grassland in The Fens we used additional sources of population density data. A complete description of the method used to estimate species population density is in Supporting Information.

The BBS involves skilled volunteers recording adult birds along 2 transects (each 1 × 0.2 km) in randomly selected 1-km squares (Harris et al. 2017). Two visits are made to each square between early April and late June. To ensure that bird survey sites covered the full range of agricultural yields, we used equivalent data from additional sites collected with the same protocol. We included existing data from National Nature Reserves and Sites of Special Scientific Interest, and conducted our own BBS surveys in 2016 and 2017. Altogether our data represent 35 sites in The Fens (5 fen, 1 wet grassland, 29 farmland) and 108 in Salisbury Plain (52 chalk grassland, 56 farmland) (mostly 1-km squares, but some larger) surveyed 2000–2017.

We accounted for different sites being surveyed in different years with generalized linear models for each species (with Poisson error structure and log link function). Maximum count in each year was the dependent variable, and site and year (both fixed factors) were independent variables. We used the natural logarithm of the species-, site-, and visit-specific effective area (detection probability × transect area [Supporting Information]) as an offset to account for species- and habitat-specific variation in detectability and then averaged (mean weighted by 1/SE) predicted site-specific species density for years 2013–2016.

Three rare breeding species, Eurasian Bittern (*Botaurus stellaris*), Common Crane (*Grus grus*), and Eurasian Stone-curlew (*Burhinus oedicnemus*), were detected too infrequently to reliably estimate detection probabilities, so we intersected data from species-specific national surveys with our survey site locations to estimate mean density per site (averaged 2013–2016).

Because wet grassland and fen were represented by only 1 and 5 bird survey sites respectively, we sought additional data on habitat-specific breeding density for 23 species identified as potentially breeding in The Fens (Balmer et al. 2013) but not detected at wet grassland or fen survey sites. We found breeding evidence for 10 species (see Supporting Information), excluding the remaining 13 from our study.

Estimating food Production Yield

We estimated total annual agricultural yield of all 4 types of spared land (fen and wet grassland in The

Fens, woodland and chalk grassland in Salisbury Plain), all farmed 1-km squares, and all bird survey sites with 4 currencies: gigajoules food energy, kilograms crude protein, value of output in British pounds, and gross margin in British pounds, all measured per hectare of unbuilt land per year (full details and estimation of monetary value in Supporting Information). We focused on energy, but results for other currencies were broadly consistent (Supporting Information).

We used the satellite-derived land-use maps described above and the 2004 Department for Environment Food and Rural Affairs agricultural census (5-km^2 resolution; http://agcensus.edina.ac.uk) to estimate the area of agricultural land uses in each site (Supporting Information). These were corrected to approximately account for crop rotations by recalculating the proportion of arable crops within a buffer (200 m in The Fens, 1100 m in Salisbury Plain) around each site, assuming within-season spatial composition of crops matches their composition across the temporal rotation (see Supporting Information). We then used the *Farm Business Survey* (data collected 2012–2015 from 55 farms in The Fens and 59 in Salisbury Plain) (Duchy College Rural Business School 2017) to estimate region- and land-use-specific yields (tons per hectare). We linked harvested products with edible end products, either consumed directly by humans or used as livestock feed, and then calculated human-edible energy and protein value based on published feed-conversion ratios (Cassidy et al. 2013) and nutritional information (U.S. Department of Agriculture 2015; Feedopedia 2017; Supporting Information). We derived equivalent yield estimates for grazed land uses (Supporting Information). Finally, we corrected our yield estimates to account for small uncropped features (not addressed in the satellite-derived land-use areas) based on the strong linear relationship between raw yield and yield calculated for a subset of sites at which uncultivated areas were manually digitized and clipped out of the areal measurements. There was a strong correlation between yields, estimated as above, and equivalent estimates derived from direct surveys of landowners (Supporting Information).

Fitting Density–Yield Curves

We fitted density–yield curves, selecting for each bird species in each region one of 2 alternative models that describe a wide range of curve shapes (Phalan et al. 2011):

$$d_i = \exp\left[b_0 + b_1\left(x_i^{\alpha}\right)\right] \quad \text{and} \qquad (1)$$

$$d_i = \exp\left[b_0 + b_1\left[x_i^{\alpha}\right] + b_2\left(x_i^{2\alpha}\right)\right], \qquad (2)$$

where d_i is the predicted density of a species at survey site i, x_i is the yield of site i, and b_0, b_1, b_2, and α are parameters estimated from the data by maximum likelihood with an iterative Nelder–Mead numerical optimization. Several parameter starting values were used to ensure that the correct solution was found (R code in Supporting Information). Following Phalan et al. (2011), α was constrained to between 0 and 4.6, and all model parameters were constrained such that the maximum predicted density did not exceed 1.5 × the maximum observed. We selected the model (Eqs. (1) or (2)) with the lowest AIC value, but avoided Eq. (2) where it predicted a sharp peak in density at $<10\%$ of the maximum observed yield (which usually resulted in density predictions of 0 at almost all feasible yields).

We fitted curves separately for each yield currency and assumed a baseline land cover of fen in The Fens ($n = 34$ sites, excluding the single wet grassland site) and chalk grassland in Salisbury Plain ($n = 108$). Wet grassland (in The Fens) and woodland (Salisbury Plain) represent alternative land covers on spared land. For The Fens, we estimated bird density in wet grassland as described above with data from the single wet grassland BBS survey square supplemented with estimates for rarer species from other sites (Supporting Information). In Salisbury Plain, given the absence of woodland survey sites, we used counts from BBS transect subsections where the dominant land cover was woodland, corrected with species-specific detection probabilities to derive average woodland densities for each species (Supporting Information).

For the 5 rare nonfarmland species listed in Supporting Information, we did not fit density–yield curves, but instead assumed populations would change in proportion to the area of their associated habitat (fen or wet grassland).

Food Production Strategies and Baseline Strategy

Each strategy delivers a food production target (P) and had 2 or 3 compartments, each with an explicit yield (Fig. 1 & Table 1). All strategies were constructed separately for each region for values of P ranging from 0.25 to 2.00 times estimated current food production.

The baseline strategy represented a hypothetical preagricultural scenario in which the entire region was unfarmed, and was used to classify species as either agricultural winners or losers. All strategies, including baseline, had 3 different land-cover compositions on spared land, varying the ratio of wet grassland:fen and woodland:chalk grassland (1:2, 1:1, and 2:1).

SIMPLE 2-COMPARTMENT STRATEGIES

We then defined a range of 2-compartment strategies (defined by the area of spared land, A_S, and the yield of farmland, Y_F), where Y_F varied from the minimum adequate yield under extreme sharing (the Y_F necessary to achieve P when $A_S = 0$) to the maximum potential yield under

Table 1. Summary of food production strategies to maintain current total production.[a]

Region	*Strategy*[b]	*P GJ km^{-2}*	*A_S km^2*	*A_F km^2*	*A_{LYF} km^2*	*Y_F GJ ha^{-1}*	*Y_{LYF} GJ ha^{-1}*
The Fens	sharing	4980	0	1206	0	49.8	–
	intermediate		446	761	0	78.6	–
	sparing		656	550	0	108	–
	3-compartment sparing		368	469	369	108	24.4
Salisbury Plain	sharing	1920	0	995	0	19.2	–
	intermediate		400	595	0	32	–
	sparing		576	419	0	45.3	–
	3-compartment sparing		442	109	443	45.3	31.8

[a] *Abbreviations: P, total production target; A_S, area of spared land, A_F, area of farmed land; A_{LYF}, area of low-yield farmland; Y_F, yield of farmed land; Y_{LYF}, yield of low-yield farmland.*

[b] *Only one intermediate strategy is shown (with Y_F halfway between that of sharing and sparing). The compartments of 3-compartment sparing are farmed land, spared land, and low-yield farmland (sharing, sparing, and intermediate strategies contain only 2 compartments—farmed land and spared land).*

extreme sparing (the maximum yield observed across all farmed 1-km squares), via 50 intermediate increments. The A_S value was adjusted such that P was maintained across all strategies (Fig. 1a) for all levels of P. The yield of spared land was fixed at the mean yield recorded in our fen, wet grassland, chalk grassland, and woodland sites (effectively a small amount of meat production).

THREE-COMPARTMENT SPARING

Three-compartment sparing involved introducing an additional low-yield farmland compartment with area (A_{LYF}) arbitrarily set as equal to the area of spared seminatural land cover (Fig. 1b). We defined this compartment's yield (Y_{LYF}, contributing to P) as the region-specific median yield at which birds with hump-shaped density–yield curves reached their maximum density (Table 1).

EVALUATING STRATEGIES

For each strategy, we then estimated each bird species' region-wide population size by multiplying the yield- or habitat-specific population density by the area of each compartment, and then summed population size across all compartments. Because the maximum potential yield was greater than in the highest yielding bird survey site in both regions, we estimated associated bird densities by extrapolating density–yield curves (or taking the highest fitted density for those species whose density–yield curve was increasing at the highest yield survey sites).

Species were classified as winners from agriculture if, at a particular food production target, their total predicted population size was greater under any food production strategy relative to the baseline scenario. Species whose population size was smaller under all production strategies relative to the baseline were classified as losers.

For each species at each food production target, we then identified the 2-compartment strategy which maximized region-wide population size. We also calculated the population size of each species under all 2- and 3-compartment strategies relative to the species' predicted population size under the current strategy (i.e. the 2-compartment strategy which matches the current area of spared land). Relative population sizes were summarized across all species with the geometric mean, with a small constant (1×10^{-5}) added to zeros to allow log transformation. We also calculated geometric mean population size separately for winners, losers, species included in the Farmland Bird Index (FBI) (Department for Food, Environment and Rural Affairs 2017) and those listed as red (>50% decline in population size or range over 25 years) or amber (>25% decline) in Birds of Conservation Concern 4 (Eaton et al. 2015).

The median R^2 of density–yield curves across species was 0.23 (IQR 0.12–0.47) in The Fens and 0.15 (0.02–0.25) in Salisbury Plain. These values are generally quite low (as expected if factors other than yield drive variation in abundance), but poor explanatory power of density–yield curves simply implies that a species is likely to be insensitive to changes across the sparing-sharing continuum. We explored uncertainty in the shape of each curve by bootstrapping; we selected survey sites at random, with replacement, from each region's pool of survey sites and fitted the density–yield functions for each species in each bootstrap sample. We repeated this process 100 times, calculating species population size and geometric mean relative population size for each sample. These results suggested density–yield curve uncertainty would be unlikely to alter our findings substantially (Supporting Information).

Results

Two-Compartment Land Sparing Versus Land Sharing

At current production levels, and assuming a 1:1 ratio of alternative land covers on spared land, 59% (95% bootstrap interval 48–64) of 101 species in The Fens achieved highest population size under land sparing, 32% (22–43) under land sharing, and 9% (6–22) under an

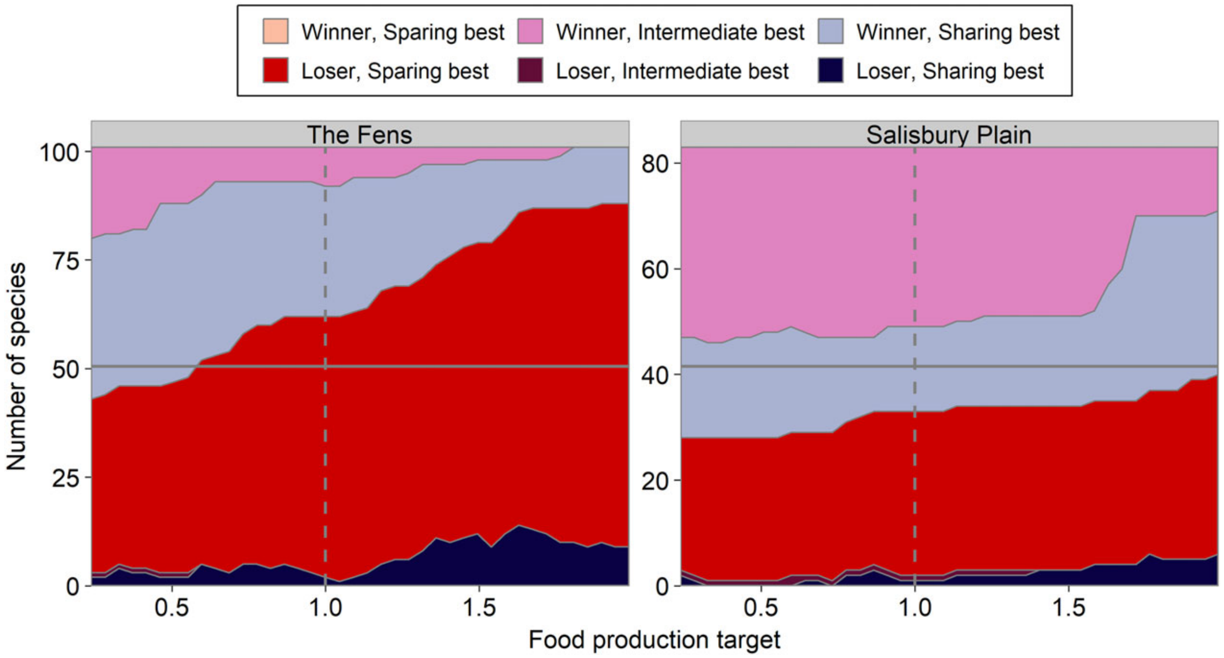

Figure 2. Proportion of species achieving maximum population size under land sparing, land sharing, or an intermediate strategy in 2 lowland areas of England (dashed vertical line, current food production target; solid horizontal line, bisects the y-axis equally; 1:1 ratio of alternative spared land-cover types assumed). Winners species (upper, pale sections) are predicted to have larger populations under a food production strategy compared with the preagricultural baseline. Losers (bottom, dark sections) are predicted to have smaller populations under all food production strategies compared with the preagricultural baseline. No winner species did best under land sparing.

intermediate strategy (Fig. 2 & Supporting Information). Most species (61% [54–70]) were classified as losers from agriculture, of which almost all (97% [83–97]) did best under land sparing.

In Salisbury Plain, the different strategies were more evenly balanced, though land sparing was still the single strategy giving the highest regional population size for most species (37% [31–54]); 20% (12–28) of 83 species did best under land sharing and 42% (24–54) under one of a range of different intermediate strategies. Only 40% (34–56) of species were classified as losers from agriculture, of which most (94% [84–99]) achieved maximum population size under land sparing (Fig. 2 & Supporting Information). Yield currency had only a small effect on these patterns, as did the definition of maximum potential yield under land sparing (Supporting Information).

In The Fens, mean relative population size across all species was maximized by 2-compartment strategies ranging from intermediate to extreme land sparing (reflecting a 4- to 13-fold increase in the area spared), whereas in Salisbury Plain mean relative population size peaked at an intermediate strategy (corresponding to about a 50% increase in spared area) (Fig. 3). Loser species had their highest mean relative population size under extreme sparing in both regions, whereas winners did best under extreme sharing in The Fens but an intermediate strategy in Salisbury Plain (Fig. 3).

Three-Compartment Sparing

The yield of the third compartment—set to the median yield at which species with hump-shaped density–yield curves reached peak density—was 53% lower than current average yield in The Fens, but 25% higher than current average yield in Salisbury Plain. In The Fens, 3-compartment sparing resulted in larger mean relative population size across all species than any 2-compartment strategy (Fig. 3). In Salisbury Plain an intermediate 2-compartment strategy resulted in slightly higher mean relative population size across all species, though bootstrap intervals overlapped (Fig. 3). In both regions, 3-compartment sparing was slightly worse than 2-compartment sparing for loser species, but much better than 2-compartment sparing for winners.

Changing the Food Production Target

As the food production target increased, the proportion of species classified as losers and doing best under land sparing increased (Fig. 2). In The Fens, 3-compartment sparing outperformed all other strategies, except at very

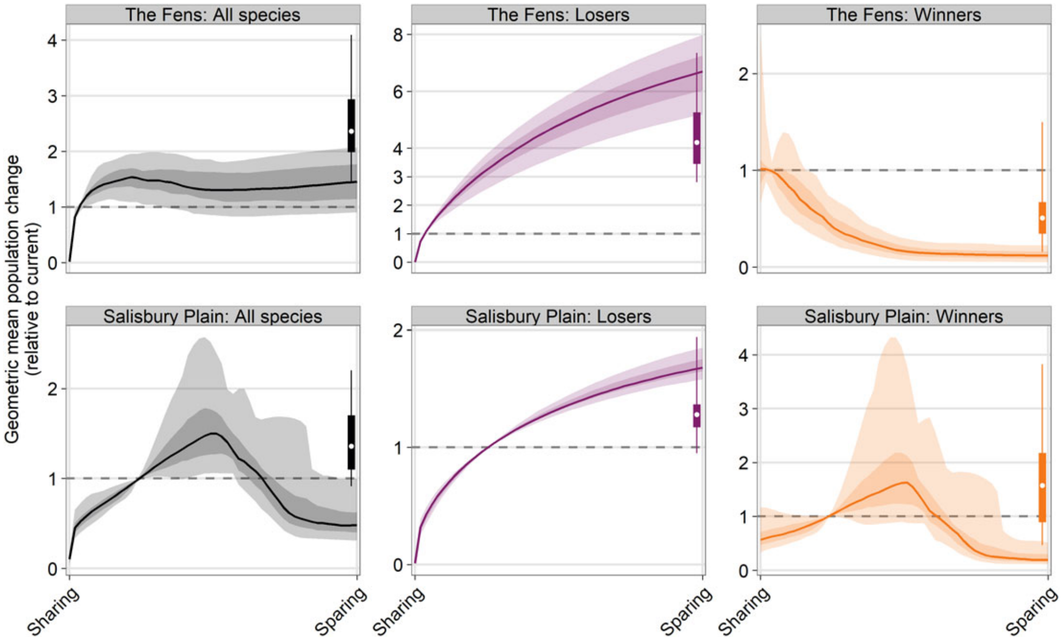

Figure 3. Geometric mean population change relative to current population size across all 2- and 3-compartment strategies for all species, species predicted to have smaller populations under all food production strategies compared with the preagricultural baseline (losers), and species predicted to have larger populations under a food production strategy compared with the preagricultural baseline (winners) in The Fens and Salisbury Plain. Results based on 100 bootstrap samples of sites, each resulting in a different species-specific density–yield curves (line, median; shaded regions, 5th, 25th, 75th, and 95th percentiles; points, bars, and whiskers, equivalent range of uncertainty for 3-compartment sparing; all strategies deliver current food production target and a 1:1 ratio of alternative spared land-cover types).

low *P* (Fig. 4). In Salisbury Plain an intermediate strategy outperformed other strategies except at high *P*, when 3-compartment sparing was best (Fig. 4).

For loser species, geometric mean population change was maximized by 2-compartment sparing under almost all values of *P*, whereas the best strategy for winners changed depending on *P* (Fig. 4 & Supporting Information). Red- and amber-listed species responded similarly to all species in both regions, with 3-compartment sparing outperforming all (in The Fens) or most (in Salisbury Plain) other strategies across all food production targets (Supporting Information). The best strategy for species making up the Farmland Bird Index varied with *P*, but was 3-compartment sparing at high production targets (Supporting Information).

Changing the Land-Cover Composition of Spared Land

Shifting the composition of spared land toward woodier land covers (fen in The Fens, woodland in Salisbury Plain) resulted in slightly more species being classified as losers doing best under land sparing (Supporting Information). The best overall strategies (based on maximizing geometric mean population change) were 3-compartment sparing with a 1:2 ratio of wet grassland to fen in The Fens and intermediate sparing with 2:1 woodland:chalk grassland in Salisbury Plain.

Discussion

As in previous studies using density–yield curves (reviewed in Balmford et al. [2015]), extreme land sparing was overwhelmingly the best strategy among losers from agriculture. These species should arguably be of high conservation concern, because they have smaller regional populations than before human habitat modification and typically smaller global ranges (Phalan et al. 2011; Hulme et al. 2013). Nonetheless, contemporary declines mean many winner species in our study regions are red listed in the United Kingdom. Averaged across all species, as well as for amber and red-listed species in isolation, our novel 3-compartment sparing strategy maximized (or came close to maximizing) geometric mean relative population size.

In contrast to loser species, winners did poorly under land sparing. In Salisbury Plain, where many birds had hump-shaped density–yield curves, an intermediate strategy (reflecting a 52% increase in spared habitat [Fig. 3]) maximized mean population change of both winners and all species combined. In The Fens, most

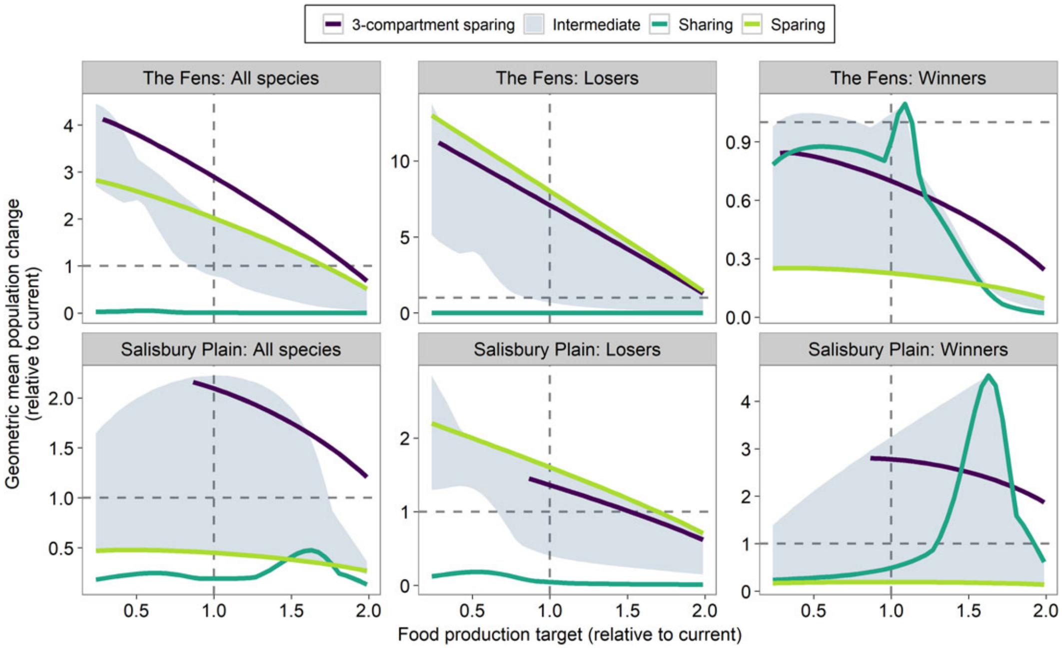

Figure 4. Geometric mean population change relative to current population size across all food production strategies and all food production targets (shading, range of outcomes associated with strategies intermediate between sharing and sparing; vertical dashed lines, current total food production; horizontal dashed lines, current mean population size; a 1:1 ratio of alternative spared land-cover types assumed). Winner (species predicted to have larger populations under a food production strategy compared with the pre-agricultural baseline) and loser (species predicted to have smaller populations under all food production strategies compared with the pre-agricultural baseline) categories are based on winner-loser status at current food production targets. At low production targets, 3-compartment sparing is not feasible because setting an equal area of spared and low-yield farmland results in the production target being exceeded.

winners did best under land sharing, showing an entirely opposite response to losers (Fig. 3). Here, increasing levels of land sparing generated diminishing returns; an intermediate sparing strategy (423% increase in spared habitat) performed similarly to extreme sparing (1296% increase in spared habitat) across all species. Three-compartment sparing performed better still by delivering some even lower-yielding farmland than land sharing while increasing the area of spared habitat by 638%. Three-compartment sparing also performed well in Salisbury Plain, where it was the best strategy at higher food production targets and very close to best for amber- and red-listed species.

Three-compartment sparing reflects a mixed approach, helping to balance the divergent interests of winner and loser species. The third compartment is targeted specifically at species with hump-shaped density yield curves (e.g. Common Linnet [*Linaria cannabina*], Stock Dove [*Columba oenas*], Grey Partridge [*Perdix perdix*]), delivering the low-yield farmland that maximizes their population density. Although 3-compartment sparing could be described as a both-and strategy, it still depends on high-yield farming to deliver the majority of the food production target. Whilst we arbitrarily set the area of the third compartment to match that of spared habitat, other optimisation-based approaches are possible (e.g., Geschke et al. 2018) and may further reconcile the trade-off between the conservation of winners and losers.

A key difference between Salisbury Plain and The Fens (and previous case studies [e.g. Kamp et al. 2015; Dotta et al. 2016]) was the relative dominance of winners in Salisbury Plain. Because losers generally achieved larger populations under land sparing and winners did not, their relative frequency shapes which strategy along the sharing-sparing continuum maximizes conservation outcomes across all species. In Salisbury Plain ~60% of species were classified as winners, perhaps reflecting the low avian diversity of chalk grassland (which supports high densities of relatively few species, such as Meadow Pipit [*Anthus pratensis*], Eurasian Skylark [*Alauda arvensis*] and Whinchat [*Saxicola rubetra*]) relative to the surrounding mixed farmland. Many winner species in Salisbury Plain are characteristic of woodlands (and benefit from hedgerows and copses in farmland), and some species classified as winners under a grassland-dominated baseline became losers under a woodland-dominated baseline (Supporting Information). The exact nature of the postglacial, preagricultural landscape in this region is debated, but palaeoecological evidence increasingly points toward a mosaic of grassland and semiopen woodland (Allen 2017; Alexander et al. 2018). Such landscapes have essentially disappeared from Britain, such that some species appear largely dependent on farming as a surrogate for extinct disturbance processes (Fuller et al. 2016). If such processes were restored on larger, wilder patches of spared land, then some species we classified as winners may instead reveal themselves as losers benefitting from land sparing.

Although we focused on breeding birds, we recognize our study regions support important overwintering populations too. Although fenland nature reserves support large numbers of nonbreeding waterbirds, several species forage on crops and residues on adjacent farmland, and it is unclear whether further intensification of this farmland would reduce habitat quality sufficiently to counteract the benefits of increasing wetland area. Likewise, we were unable to consider regionally extinct species or those likely to colonize in response to climate change or the provision of larger tracts of seminatural areas, though protected areas (whose extent would presumably increase under land sparing) are key for new U.K. colonists (Hiley et al. 2013). Taxa other than birds may respond differently, but researchers using the density–yield approach have discovered that insects and plants are frequently more sensitive to disturbance than birds; sparing outperforms sharing in both agricultural (Phalan et al. 2011; Williams et al. 2017) and urban (Soga et al. 2014) contexts.

Finally, although land sparing implies the separation of biodiversity from food production, yields (and their long-term resilience) may be maintained or enhanced by the promotion of service-providing biodiversity within farmed landscapes (Blaauw & Isaacs 2014; Pywell et al. 2015). To the extent that biodiversity boosts yields, land sparing and ecological agriculture are entirely compatible. Similarly, it may be possible to depart from observed density–yield relationships and increase biodiversity without incurring a yield penalty. However, many species are agriculturally nonfunctional (Kleijn et al. 2015) and may provide ecosystem disservices (e.g., Grass et al. 2017). As a conservation strategy, land sharing is likely therefore to be associated with some yield penalty, resulting (for any given level of food production) in an exported environmental footprint as food demand is met elsewhere. Still, the principals of sustainable intensification (Godfray & Garnett 2014) should be central to any land sparing strategy (Phalan 2018); food production must be sustainable in the long-term, and environmental externalities should be limited. Recent research suggests, however, that when externalities are expressed per unit product rather than per unit area, high-yielding practices can outperform low-yielding ones (Balmford et al. 2018).

Our results add to studies from elsewhere by showing that in Europe the benefits of protecting or restoring large areas of seminatural or natural land cover can be augmented by also managing significant areas under low-yielding farmland. Affording both types of conservation area while maintaining overall production relies (if food imports are not to rise) on encouraging high-yield production. This underscores the crucial importance for delivering conservation objectives of identifying resilient, sustainable methods of boosting farm yields, and of finding mechanisms whereby yield increases on farmed land are accompanied by the protection or restoration of other areas primarily for conservation (Phalan et al. 2016).

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Supporting Information

Methods to estimate bird densities (Appendix S1) and yields (Appendix S2), supplementary figures and tables (Appendix S3), and R code for density–yield curves (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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