Farming and the Fate of Wild Nature

Rhys E. Green,1,2* Stephen J. Cornell,1,3 Jörn P.W. Scharlemann,1,2 Andrew Balmford1,4

1Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK. 2Royal Society for the Protection of Birds, The Lodge, Sandy, SG19 2DL, UK. 3The Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK. 4Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Private Bag, Rondebosch 7701, South Africa.

* To whom correspondence should be addressed. E-mail: reg29@hermes.cam.ac.uk

World food demand is expected to more than double by 2050. Decisions about how to meet this challenge will have profound effects on wild species and habitats. We show that farming is already the greatest extinction threat to birds (the best known taxon), and its adverse impacts look set to increase, especially in developing countries. Two competing solutions have been proposed: wildlife-friendly farming (which boosts densities of wild populations on farmland, but may decrease agricultural yields), and land-sparing (which minimises demand for farmland by increasing yield). We present a model that identifies how to resolve the trade-off between these approaches. This shows that the best type of farming for species persistence depends on the demand for agricultural products and on how the population densities of different species on farmland change with agricultural yield. Empirical data on such density-yield functions are sparse, but evidence from a range of taxa in developing countries suggests that high-yield farming may allow more species to persist.

Clearance for cropland or permanent pasture has already reduced the extent of natural habitats on agriculturally useable land by more than 50% (1-3) and much of the rest has been altered by temporary grazing (4). Intensive management to increase production – through irrigation and the application of fertilizers and pesticides – can further reduce the wildlife value of farmed land. Although growth in global food production outstripped population growth between 1961 and 1999, this was achieved through a 12% increase in the global area of cropland and a 10% rise in the area of permanent pasture (2, 3). Overall food crop yield per unit area (3) grew by 106%, but this was linked to a 97% rise in the area of land under irrigation, and 638%, 203% and 854% increases, respectively, in the use of nitrogenous and phosphate fertilizers and the production of pesticides (2, 5, 6). These impacts look set to grow still further (5). With the human population predicted to rise to 8-10 billion (7, 8) and with rapidly increasing per capita consumption (9), overall food demand is expected to increase two- to three-fold by 2050 (6, 10). In this paper we propose an agenda for the research needed to identify how this enormously increased demand can be met at the least cost to the other species with which we share our planet.

Agricultural change: A tale of two worlds. From the perspectives of both development and conservation, globally averaged changes in agriculture mask important spatial variation, with recent changes being more pronounced in the developing world, where most species occur. For instance, since 1961 the total area of cropland in the developing world has increased by over 20%, while developed world cropland area has shrunk (Fig. 1A). A similar pattern emerges for permanent pasture (Fig. 1B). These differences in the rates of change of farmland area are not offset by lower yield growth in developing countries. Crop yields (3) have grown steadily in both the developing and developed world, with the former lagging the latter by an average of roughly 20 years (Fig. 1C). Annual growth in yield is now higher in the developing world. Further evidence that farming is changing faster in the developing world comes from trends in livestock production. Because of increasing domestic demand (9), per capita meat production is rising rapidly in the developing world, whereas elsewhere it is declining; more than half of global meat production now takes place in developing countries (Fig. 1D). How are these changes impacting wild habitats and species?

Differing impacts of farming on wild nature. Several kinds of data suggest that, while it is an important driver almost everywhere, the effect of agricultural change on wild nature is now greatest in developing countries. Coarse-scale evidence of changes in forest cover shows that recent net gains in temperate and boreal forest cover are more than offset by continued losses in tropical regions, largely by conversion to agriculture (11). Patchy data on changes in populations of temperate and tropical forest vertebrates confirm this pattern (12, 13). For a more detailed picture of the relative importance of threats to biodiversity posed by farming, we used BirdLife International’s World Bird Database (3) to dissect the problems faced by all 1923 species
of globally threatened and Near Threatened birds; data for no other taxa permit such detailed and comprehensive analysis.

These data show that farming (including conversion to farmland and its intensifying use) is the single biggest source of threat to bird species listed as threatened (accounting for 37% of threats) and is already substantially more important for species in developing than developed countries (40% and 24% of threats respectively, Fig. 2A). For developing and developed countries, alike the scale of the threat posed by agriculture is even greater for Near Threatened species (57% and 33% of threats respectively, Fig 2B). Since these are likely to become threatened in the near future (14), this implies that agriculture is a growing threat to bird species. There are also larger absolute numbers of threatened and Near Threatened species in developing than developed countries (threatened 1039 vs 225 species, Near Threatened 687 vs 95) Taken together, these data indicate that agriculture is the major current and likely future threat to bird species, especially in developing countries. Given the growing scale and impacts of agriculture, how should we best resolve the need for increased food production with the desire to minimize its impact on what remains of wild nature? Two sorts of suggestions predominate.

Wildlife-friendly farming. Many conservation biologists argue that the global application of wildlife-friendly farming methods would reduce the impact of agriculture on biodiversity. Approaches include the retention of patches of natural habitat and extensively-farmed semi-natural habitats within the countryside, and farming in ways that minimize the negative effects of fertilizers and pesticides on non-target organisms (15–20). Such wildlife-friendly farming receives particularly strong support in Europe, where evidence of declines in the previously high biological value of long-established agroecosystems (17, 21, 22) is used to justify agri-environment payments to European Union farmers worth over $2.7 billion each year (23). There are far fewer data on farmland biodiversity in less developed regions, but evidence that around half of Costa Rica’s native forest species of birds, mammals, butterflies, and moths also occur in agricultural areas (table S1) has been used to argue that maintaining low intensity agriculture will benefit biodiversity in developing countries as well (18–20; see also (table S1).

It is clear that adopting farming methods that enhance population densities of wild plant and animal species on farmland is beneficial to biodiversity, provided that the change to wildlife-friendly farming does not require a reduction in crop yield (19, 24). However, it is frequently observed that the biodiversity value of farmland declines with increasing yield [e.g. (17, 21, 22)], which suggests that maintaining high wildlife interest on farmland often requires that opportunities for high crop yields are foregone. The fact that existing agri-environment schemes depend on farmers receiving large amounts of financial compensation for lost production demonstrates that such yield penalties are perceived as real. Their existence underlies a very different school of thought on how best to simultaneously deliver food production needs and meet conservation goals.

Land-sparing. This second approach hinges on moving beyond thinking solely about the farmed landscape to considering the consequences of yield penalties for the total area of farmed versus non-farmed land. While wildlife-friendly farming is beneficial on farmland, if it reduces yields then a larger area must be farmed in order to meet any given production target. Both the Costa Rican and other (table S1) results show that even under benign agriculture, farmland usually hosts far fewer species – especially those of conservation concern – than do the relatively intact habitats from which it was derived. Hence if yield penalties from wildlife-friendly farming are sufficiently large, it is possible that the best route to meeting both food production and conservation goals may be to increase yields on already converted land, thereby reducing the need to convert remaining intact habitats, and potentially freeing-up former farmland for restoration to a more natural state.

This land-sparing argument is rarely made by conservationists (25, 26), but is widely advocated in the agriculture and development literature (27–33). Retrospective calculations for the USA, China and India suggest that, without the dramatic increases in yields seen over recent decades, producing the amounts of food currently grown there would require 2 to 4 times more land under crops than at present (28, 33–35). Moreover, comparisons among Latin American countries provide empirical evidence that, taking other factors into account, land-sparing has occurred: in the 1980s, countries whose agricultural yield was higher had lower deforestation rates (30) and those whose yield increased more had lower rates of increase in farmland area (27). Finally, prospective calculations show that without yield increases, even maintaining current per capita food consumption would necessitate a near-doubling of the world’s cropland area by 2050; by comparison, raising global average yields to those currently achieved in North America could result in very considerable land-sparing (28).

Hence, while wildlife-friendly farming offers scope to increase the biodiversity value of farmed land on a per unit area basis, this may not result in a net benefit to biodiversity if it reduces crop yield. On the other hand, increasing yield could reduce the requirement for farmland and the rate of conversion of currently non-farmed land. We may therefore face a choice, between having a greater area of low-yielding wildlife-friendly farmland and less intact habitat, or having a smaller area of high-yielding, less wildlife-friendly farmland and more area available for wild nature elsewhere.
Identifying the key parameters that can resolve this trade-off requires a model.

**Modeling the trade-off.** Our model relates the population size of individual species within a large area (“province”) to the yield per unit area of farmed land and the target agricultural production required. We focus on one species at a time to allow for evident differences between species in how they respond to changing agricultural activity. Results can later be combined across species and used to optimize province-wide metrics such as the proportion of species committed to extinction. The model province consists of a farmed part (which can include patches of natural habitat) and a non-farmed part, and is uniform in its potential suitability for both farming and the species of interest. We ignore any negative external effects of farming on wildlife in non-farming areas. Crop yield \( y \) of the farmed land is scaled relative to the maximum attainable over a large area, and the target level of production of agricultural goods \( \alpha \) is assumed to be fixed and is scaled in terms of the proportion of the province needed to grow it if yield was at the maximum (i.e. at \( x = 1 \)). The minimum yield that can still produce the production target is \( x = \alpha \) (because the whole of the province must be farmed to grow the target at this yield), and the permissible yield lies in the range \( \alpha \leq x \leq 1 \). For a given yield \( x' \) within this range, we assume that the production target is just met, so that the proportion of the province that is farmed is \( \alpha/x' \) and the proportion that is non-farmed is \( 1 - (\alpha/x') \).

To see how yield then affects the population of a given species, consider a species-specific density-yield function, whereby population density is some function \( f(x) \) of yield, and is scaled to 1 on non-farmed land \((f(0)=1)\). The overall population of a species across the whole province is then the sum of its population on non-farmed land \( 1 - (\alpha/x') \) and its population on farmed land \( f(x')/(\alpha/x') \), which is \( 1 + (\alpha/x') \) \((f(x') - 1)\). Considering first a concave density-yield function (Fig. 3A, red curve), highest-yield farming (at \( x = 1 \), summarized in the left panels) is associated with very low relative population density on farmed land (star in Step 2), but with a large area of non-farmed land with relative population density of 1 (Step 3), containing most of the total population (Step 4). In contrast, farming at the lowest permissible yield \( (x = \alpha, \text{right panels}) \) results in a far higher density on farmed land than with high yield farming (star in Step 2), which in this case more than offsets the loss of population associated with having no non-farmed land. For this density-yield function, the total population size of this species is thus higher with lowest-yield than with highest-yield farming. Working through the same logic with a convex density-yield function (Fig. 3B), it can be seen that the population density on lowest-yield farmed land is now considerably lower than with the concave function, and the total population is higher with highest-yield farming (the sum of few individuals on farmed land plus many on the non-farmed land spared from conversion). Comparison of these two examples therefore illustrates that the shape of a species’ density-yield function affects which farming regime maximizes its overall population.

To explore the effects of different density-yield functions more systematically, consider a graphical version of the model (Fig. 4A). This includes both a density-yield function (red curve) and a vertical threshold line (in black) at \( x = \alpha \), representing the minimum yield that can meet the production target. For any given yield \( x' \) in the permissible range \((\alpha \leq x' \leq 1)\), it can be shown that the \( y \)-value at which a chord drawn from \( x = 0, y = 1 \) to the red curve \([at x', f(x')]\) intersects the vertical threshold line gives the total population size of the organism at \( x' \), summed across the entire province and scaled relative to that if the entire province was non-farmed \([\alpha \leq x' \leq 1 + (\alpha/x') (f(x') - 1)]\). By considering where all such permissible chords intersect the vertical threshold one can then identify the yield at which total population size is maximized.

Thus in Fig. 4A (corresponding to Fig. 3A), the chord for lowest permissible yield (in green) intersects the vertical threshold above the line for maximum yield (in blue, termed the critical chord), and all other chords. Indeed, whenever the \( f(x) \) curve is concave between \( x = 0 \) and \( x = 1 \), then the chord for lowest permissible yield always cuts the vertical threshold at the highest point of any yield in the permissible range: thus the total population of the species is highest at lowest possible yield. On the other hand, if as in Fig. 4B (corresponding to Fig. 3B), the \( f(x) \) curve is convex between \( x = 0 \) and \( x = 1 \), the critical chord always cuts the vertical threshold above all other permissible chords and farming at the maximum yield results in the highest population of the species. This rule also applies for species whose density increases with increasing yield (fig. S1). Results for more complex density-yield functions include dependence of the optimum on \( \alpha \), and an optimum at yields intermediate between the minimum and maximum (supporting online text).

**Extension from individual species to province-wide biodiversity.** Our model offers a quantitative comparison of the benefits to biodiversity of wildlife-friendly farming and land-sparing, and highlights the fundamental importance of the shape of density-yield functions. It can be extended from the single species case by considering density-yield functions for all species, or a representative sample, in order to estimate a province-wide metric such as the proportion of species committed to extinction under a particular farming regime. Those species whose density-yield functions exceed 1 at the selected yield value would be assumed not to be at risk of extinction because they would have higher total populations under that regime than before agricultural modification of the landscape. For species whose total population is lower than if
the whole province was non-farmed (because their density is lower on land farmed at the chosen yield than on non-farmed land), extinction risk might be calculated using methods derived from the species-area relationship (36). One could then calculate an optimal farming regime, which minimizes the proportion of species committed to extinction (but which would nevertheless be less favorable for some species than for others).

**Limitations.** However, despite these potentially valuable applications, the model can be criticized for being much simpler than the real world, in various ways. First, our model assumes that farming does not affect the population density of species in non-farmed areas. High-yield farming often leads to external effects such as pollution from pesticides and fertilizers and abstraction of water for irrigation (5, 6). However, such adverse effects can be reduced, through a combination of technical development and regulation (6, 24, 32, 37). Furthermore, low-yield farming may also affect non-farmed habitats and, although the effect per unit of farmed area may be less severe, the total impact might be greater than for high-yield farming if larger areas of farmland are needed to meet a production target.

Second, the model supposes that agricultural production is at a fixed level for a given scenario, so that an increase in yield results in a proportionately reduced area required for farming. In practice, both empirical and theoretical evidence suggests that land-sparing can sometimes be imperfect. If product demand or labor supply are elastic, or if technological changes free up rather than use up labor, increasing yields can in effect increase production targets, thereby adding to the requirement for agricultural land (24, 31, 38). The model also assumes that non-farmed land spared from agricultural use will not be converted to some other human use unfavorable for biodiversity. Offsetting these points about likely imperfections in the operation of land-sparing, it is also worth noting that there are imperfections in the real world in the delivery of biodiversity benefits by wildlife-friendly farming techniques (39).

Last, the model assumes that population size is given simply by the product of density and area. The size and distribution of patches of farmed and non-farmed land are ignored, but fragmentation of preferred habitat would be expected to influence population density and viability. We also ignore dispersal between farmed and non-farmed land, yet because of the effects of habitat quality on demographic rates, the population in one compartment might only persist because of net immigration from the other (40).

Nevertheless, while the model could be elaborated to incorporate externalities, imperfect land-sparing, the spatial configuration of different land-use patches and source-sink dynamics, we consider that our main conclusion would hold—that the best way to reconcile farming and conservation depends on actual production targets and, crucially, on the relative frequency of species with different density-yield functions.

**Prospects for wildlife-friendly farming vs land-sparing.** At present we know little about how species’ population densities on farmed land change with yield, though some forms of the density-yield function seem unlikely to be frequent (supporting online text). Few studies have measured density comparably across a range of production regimes, and fewer still have simultaneously measured agricultural yields. Nevertheless, the growing number of studies indicating that half or more of all species of unmodified habitats are absent even from low-intensity farmland (table S1) suggests that many species are likely to exhibit negative-trending convex density-yield functions (Fig. 4B). These species will fare best under maximum-yield agriculture combined with land-sparing. Such beneficial land-sparing is perhaps easiest to envisage in developing countries with limited histories of farming and large numbers of agriculturally-naive species, where increasing yields may reduce the pressure to clear intact habitat. However, insofar as valuable wildlife habitat can be restored or recreated on abandoned farmland, and agriculturally-sensitive species still exist, land-sparing through yield increases may also be important in regions with long histories of agriculture: indeed, coupling appropriately-managed intensification with abandonment and restoration elsewhere may be a principal route to achieving new and ambitious programs of large-scale habitat recovery in Europe and elsewhere (41–43).

**An agenda for empirical research.** What kinds of farming give the best prospect of minimizing losses of wild nature to habitat removal and change whilst providing food for a growing and more demanding human population? This paper does not provide an answer to that question. However, it does make explicit the nature of the quandary about whether high-yield or low-yield farming, or something in between, is best for biodiversity. Above all, our analysis highlights the need to know more about density-yield functions of real species in the real world, about how they might be modified by changes in agricultural and conservation methods, and about how far different kinds of farming influence the wildlife of non-farmed areas. We also need to know much more about the extent and limits to which land is spared from agricultural use because of increased yields. Rapidly acquiring the data to address these issues is essential if we are to make wise and informed choices about how and where we farm. Few other decisions will have as great an influence on the fate of wild nature.
References and Notes
3. Materials and methods are available as supporting material on Science Online.
41. RSPB, Futurescapes: Large-scale Habitat Restoration for Wildlife and People (RSPB, 2001).
44. We thank Mark Avery, Justin Brashares, Tom Brooks, Gretchen Daily, David Gibbons and Bryan Grenfell for discussion and Ali Stattersfield, Martin Sneary and Mark Balman for access to the World Bird Database. S.J.C. acknowledges funding from the Wellcome Trust.
Materials and Methods
Figs. S1 and S2
Table S1

5 October 2004; accepted 30 November 2004
Published online 23 December 2004;
10.1126/science.1106049
Include this information when citing this paper.

Fig. 1. Changes in agriculture in the developing and
developed worlds (3), 1961-2000, showing annual changes in
cropland (A), permanent pasture (B), mean crop yields for the
23 main food crops (3) (C), and per capita and total meat
production (D). In (A) and (B) farmed areas are plotted as a
% of useable land (3). Filled symbols are for developing
world, open for developed. In (D) circles are for per capita
meat production, diamonds for total meat production.

Fig. 2. The mean proportion of a species’ listed threats that
are attributable to agriculture plotted for threatened (A) and
Near Threatened (B) birds from the developed (white) and
developing (black) world (3).

Fig. 3. Essential features of the model relating species
population size to agricultural yield, illustrated by two
examples In the first (A), a province, shown as a map (A1), is
composed of farmed (yellow) and non-farmed (green) land
The target agricultural production $\alpha = 0.2$, which could be
achieved by highest-yield farming on 20% of the land area ($x$
= 1, left panels) or by farming all the land at lowest possible
yield ($x = 0.2$, right panels) The organism exhibits a concave
density-yield function (red curve in A2), with its highest
population density on non-farmed land (where it is set to 1)
and far lower density under highest-yield farming than under
lowest-yield farming (compare stars on left and right panels
in A2). The total population size of the whole province can be
visualized by shading the maps (A3), so that for each habitat,
the vertical extent of hatching is proportional to relative
population density. The summed area of the hatched zones,
relative to that of the whole province, then gives the total
population size relative to that if the whole province was
unfarmed. These relative population sizes, for non-farmed
and farmed areas and the province as a whole are shown in
the histograms (A4). In this case, the total population is
higher with lowest-yield farming. In the second example (B),
the situation is the same, except that the density-yield
relationship is convex. In this example, the steep drop in
density even at low yields means that land-sparing is
worthwhile and the total population is higher with highest-
yield farming.

Fig. 4. A graphical version of the model. (A) A concave
density-yield function $y = f(x)$ (red curve; same as Fig. 3A2).
The vertical threshold line (black) shows the minimum yield
that can meet the target agricultural production ($\alpha = 0.2$). A
chord drawn from $x = 0, y = 1$ to the red curve at $x'$, $f(x')$ at
any point in the permitted range $\alpha \leq x' \leq 1$, intersects this
vertical threshold at $1 + (\alpha / x') (f(x') - 1)$, which is the total
population size of the organism in the entire province scaled
relative to that if the entire province was non-farmed (see
text). The blue line (termed the critical chord) joins the points
on the red curve for $x = 0$ and $x = 1$; its intersection with the
vertical threshold (blue square) gives relative population size
under maximum yield farming. The green line runs from $x =
0, y = 1$ to the red curve at 0.2, $f(0.2)$ and so its intersection
with the vertical threshold (green square) gives the relative
population size at lowest possible yield; this is greater than
that under highest-yield farming, and indeed that of any other
chords in the permitted yield range, so total population size is
maximized under lowest-yield farming. These results are the
same as those obtained in steps A1 – A4 of Fig. 3. (B) Same
as (A), except that the convex function from Fig. 3 B2 is used
(with the same results as steps B1 – B4). This time the critical
chord cuts the vertical threshold above the green chord and
any other permissible chords, so the total population is
highest when yield is highest.