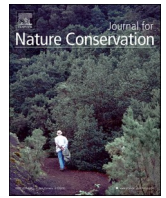


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# The cost of stabilising the German lapwing population: A bioeconomic study on lapwing population development and distribution using a cellular automaton

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## ABSTRACT

The populations of farmland birds such as the lapwing (*Vanellus vanellus*) are declining sharply. These populations suffer from frequent cultivation measures and degraded habitat quality on arable land. An effective conservation measure is the lapwing plot, an agriculturally unused section within an arable field. We address German lapwing population development and dispersal if different shares of the population are safeguarded by the use of lapwing plots. We adapted a matrix projection model and extended it by projecting population development in three different habitat types (arable land, grassland and optimal habitat) and in varying scenarios. We introduced a cellular automaton and developed a new algorithm to simulate dispersal dynamics. The results show that without further conservation measures, the population could decline from 70 000 breeding pairs in 2006 to 12 000 or 23 000 pairs in 2055, depending on the underlying assumptions. Our model can be used to set environmental goals and then simulate the necessary implementation levels of conservation measures, such as the lapwing plot, and estimate the corresponding costs. For the goal of at least stabilising the population, 60% of the pairs in the normal agricultural landscape need to be safeguarded. For the population on arable land the corresponding costs range between 1.6 and 2.8 million € per year.

## 1. Introduction

Growing evidence suggests that biodiversity in the agricultural landscape is declining sharply. For farmland birds, this is well documented in the European Union (EU), where the population of farmland birds decreased by 30 % between 1990 and 2015 (German National Academy of Sciences Leopoldina, acatech, 2020). The lapwing (*Vanellus vanellus*) is a farmland bird that has experienced a particularly strong decline. The lapwing is an indicator species, as designated in the German indicator for 'Biodiversity and landscape quality' developed in the National Sustainability Strategy (German Federal Agency for Nature Conservation, 2021). In Germany, the lapwing population decreased by more than 80 % between 1990 and 2018 (Kamp et al., 2021). This decline is mainly due to an intensification of agriculture and an increase in predation (Plard et al., 2019). The lapwing's preferred breeding habitat in the farmed landscape is extensively managed open, wet grasslands. However, the species also breeds in dry habitats such as dry grasslands and arable fields (Shrubb, 2009), especially when extensively

managed grassland is lacking on a landscape scale. On both grassland and arable land, intensive agricultural management leads to habitat abandonment, a high risk of nest destruction and low chick survival rates. For successful reproduction, intensively managed grassland is often too dense and mown too frequently, while on arable land, the vegetation structure of autumn-sown crops is too high and too dense, and in spring crops, especially maize, mechanical cultivation measures are either 'badly' timed or too frequent (Kamp et al., 2015; Roodbergen, van der Werf, & Hötter, 2012). Moreover, habitat quality is degraded because of grassland drainage and low food availability, i.e., declines in invertebrate biomass induced by fertiliser and pesticide use (Benton, Bryant, Cole, & Crick, 2002; Boatman et al., 2004; Kentie, Hooijmeijer, Trimbos, Groen, & Piersma, 2013; Sánchez-Bayo & Wyckhuys, 2019; Schekkerman & Beintema, 2007). Habitat degradation also raises the chicks' vulnerability to predators, which have simultaneously increased in density (Roodbergen et al., 2012; Schekkerman, Teunissen, & Oosterveld, 2009).

The European Commission's current strategy papers, such as the

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Farm to Fork Strategy (European Commission, 2020a) and the European Green Deal (European Commission, 2019), are strongly committed to combating biodiversity loss, especially in agricultural landscapes. In the Biodiversity Strategy for 2030, the status of farmland bird populations is considered to be an important indicator for the ecological status of agroecosystems, and it calls for action to stop and reverse the decline (European Commission, 2020b). The Strategic Plan Regulation of the upcoming EU Common Agricultural Policy (CAP) for the funding period 2023–27 requires that member states formulate environmental targets for so-called impact indicators and strategies for achieving the intended levels (“new delivery model”) (Art. 5, 6, 7 European Parliament and Council, 2021/2115). These impact indicators include “I. 19 Increasing farmland bird populations” and “I. 20 Enhancing biodiversity protection” (Annex I European Parliament and Council, 2021/2115). In addition, the European Commission alleviates the legal pressure on member states to achieve legally agreed environmental objectives (e.g., Habitat Directive) not only with respect to the preservation of abiotic resources (nitrate pollution) but also with respect to biotic resources, i. e., lawsuits for insufficient protection of habitats (Court of Justice of the European Union, 2011; European Commission, 2020c; 2021).

The provision of lapwing plots is one of the most effective measures for the conservation of lapwings on arable land (Cimioti et al., 2022; Sheldon, Chaney, & Tyler, 2007). As these plots are undisturbed throughout the breeding and hatching season, they provide food and shelter, especially for lapwing chicks but also for other farmland bird species (skylark (*Alauda arvensis*), corn bunting (*Emberiza calandra*), yellowhammer (*Emberiza citrinella*), and linnet (*Linaria cannabina*)), as well as other taxa, such as butterflies (*Lepidoptera*), bumblebees (*Bombus*) and mammals such as brown hares (*Lepus europaeus*) (MacDonald, Maniakowski, Cobbold, Grice, & Anderson, 2012). The use of lapwing plots was shown to contribute to breeding success in terms of fledglings per breeding pair in several studies (Hoodless & MacDONald, 2014; MacDonald et al., 2012; Schmidt et al., 2017; Sheldon et al., 2007). This practice requires the farmer to idle larger areas of arable land, resulting in considerable income losses for farms, especially when applied on a landscape scale.

In the EU, protection measures such as the lapwing plot can be implemented through voluntary agri-environmental schemes (AES). The basic idea of AES is that farmers are financially compensated on the basis of costs incurred and income foregone when implementing such measures on their fields. In the CAP 2023–27, the member states shall determine payment levels for farmers with respect to the expected ambition level for environmental targets (Art. 70 (4) European Parliament and Council, 2021/2115). Against this background, it is important to specify the environmental objective of a protection measure, e.g., lapwing population size, and to estimate the corresponding costs.

Our study addresses the following research questions: How will the lapwing population in Germany and its distribution develop if land use remains stable and no additional conservation measures are taken? What percentage of the population needs to be covered by conservation measures such as lapwing plots to stabilise or increase the lapwing population? How many hectares of lapwing plots are necessary for this, and what are the costs involved?

The study is structured as follows. Section 2 summarises the current state of research with regard to projecting future lapwing populations and shows how our work differs from previous studies in aim and methodological approach. Section 3 provides a summary of our methods and the data used. A detailed description is given in the Technical Annex. In Sections 4 and 5, we present and discuss this study’s results, respectively. Concluding remarks in Section 6 elaborate on the main findings and how our approach could be used for planning and ex ante evaluation of agri-environmental schemes implementing the lapwing plot.

## 2. State of research

Most previous studies that project future population trends work with statistical models (mainly linear mixed effects models) that quantify the influence of land-use change on population abundance. Within those studies, space-for-time approaches are a common tool to compensate for a lack of long-term land use and bird data by assuming that differences between localities are equivalent to differences between dates (Pickett, 1989). Population developments are then forecasted on the basis of future land use predictions (Chiron, Princé, Paracchini, Bulgheroni, & Jiguet, 2013; Scholefield et al., 2011). For lapwing population development in Germany, different authors present contrasting results. Sauerbrei, Ekschmitt, Wolters, and Gottschalk (2014) project the effects of increased maize cultivation for bioenergy production induced by the German Renewable Energy Act. According to their results, the populations of several farmland bird species would decline, whereas the population of lapwings would increase. The results are corroborated by Jerrentrup et al. (2017), who conclude that the increased number of maize fields do not particularly affect field nesters (including lapwings). However, Sauerbrei et al. (2014) critically discuss that their model predicts only the abundance of adult birds and not population growth determined by, for example, breeding success, which is limited in maize fields. In contrast, Busch et al. (2020) identify the increase in energy crops, such as maize and rapeseed, as the most important factors in the decline of lapwings, along with the increase in winter wheat and the transformation of fallow land into intensively used cropland. The driving policy decisions behind these changes are the promotion of bioenergy (renewable energy law) and the abolishment of the mandatory set-aside for farms receiving support via the CAP in 2007.

Plard et al. (2019) project future lapwing population development for the entire Dutch population and one for three sites in the German federal state of Schleswig-Holstein, each based on a separate integrated population model. The models include demographic parameters such as survival and productivity (number of fledglings per breeding pair), which allows the projection of population growth from one year to the next. In comparison to the studies mentioned above, land use is not directly included in the models but is reflected in the demographic parameters. The results show that the low level of productivity is the most important driver for the continuous decline in both populations.

Roodbergen et al. (2012) draw the same conclusion in their meta-analysis of Europe-wide data on demographic parameters, namely, that population declines are mainly caused by reduced productivity. For Western Europe, their results also suggest that the main causes of reduced productivity, such as agricultural intensification, began to take effect as early as the 1950s. Productivity values declined until 1990 and then stabilised or even recovered slightly, but only at such a low level that they still cannot compensate for adult mortality.

Souchay and Schaub (2016) show that survival probabilities for three major European breeding regions are quite constant. They also conclude that the loss of population is largely due to a decrease in productivity caused by land use changes.

We pursued a somewhat different goal than the abovementioned works. In addition to the influence of land use change, the extent of conservation measures also plays a decisive role in the population development of a species that is specifically bound to anthropogenic land use, such as the lapwing. We therefore performed a population viability analysis (PVA) to research the impact of conservation measures. PVAs are simulation models based on demographic data to enable conservation management decisions for endangered species (Beissinger & Westphal, 1998; Chaudhary & Oli, 2020). Among the different types of PVA, we used a spatially explicit population model combining “a population simulator with a landscape map that describes the spatial distribution of landscape features” (Wiegand, Naves, Stephan, & Fernandez, 1998). We analysed how to achieve different environmental goals (i.e., population stabilisation and increase) with different levels of implementation of conservation measures. We further combined the

PVA with an economic analysis as we also calculated the corresponding costs. For this reason, we modelled the population results spatially explicitly, as the costs for compensating farmers (gross margins) vary greatly from region to region.

### 3. Data and method

Our approach was to combine a simulation of spatial population distribution with a temporally explicit population model, i.e. population development is predicted for the period from 2006 to 2055. This chapter provides a summary of the data used in the model and the methods applied. A detailed description is given in the Technical Annex (Appendix A). We transferred the matrix projection model from [Plard et al. \(2019\)](#) into the programming language R (Version 1.4.1717, [R Core Team, 2021](#)) and extended it by differentiating population growth in three different habitats: arable land, grassland and optimal habitat. Definitions of the habitat types are given in Section 3.1.1.1. Thus, as in [Plard et al. \(2019\)](#), land use is not directly included in the model, but it is reflected in the demographic parameters, which we assume to be constant over time but to differ among the habitat categories. We expanded the model by simulating the dynamics of population dispersal with a cellular automaton (also in R). Programming cellular automata is a tool in ecological modelling ([Balzter, Braun, & Köhler, 1998](#); [Dytham, 1995](#); [Eide, 2012](#); [Ellison & Bedford, 1995](#); [Silvertown, Holtier, Johnson, & Dale, 1992](#); [Soetaert & Herman, 2009](#)) including PVAs ([Beissinger & Westphal, 1998](#)), but to our knowledge, it is applied here for the first time on a lapwing population.

With the model, we reproduced the past population developments for the whole area of Germany, divided into three regions. On the basis of the past developments, we projected both a future ‘business as usual’ scenario (without additional conservation) and scenarios with additional conservation measures, i.e., lapwing plots. Finally, we calculated the costs and the required hectares for lapwing plots to implement the conservation measure scenarios.

#### 3.1. Data

##### 3.1.1. Attributes and initial state of the cells

For the cellular automaton, we divided the German federal territory into 4 698 (81 × 58) cells. The cells are approximately 10 × 10 km each and correspond to the grid cells of the Atlas of German Breeding Bird Species (ADEBAR) ([Gedeon et al., 2014](#)). The ADEBAR cells are based on ordnance sheets of the topographical map 1:25 000, which were transformed to a Gauss Krüger projection. In addition, each cell may contain up to three habitat types: arable land, grassland and optimal habitat.

**3.1.1.1. Habitat area.** In the first step, we estimated the available potentially suitable habitat areas per cell and habitat type (arable land, grassland, optimal habitat) using PostGIS (Version 3.0.0). We followed the assumption that all areas are suitable as breeding habitats if they are not explicitly defined as “unsuitable” (=exclusion areas). Exclusion areas are, for example, tree-covered areas, transport areas (roads, parking lots, railways) or areas located at altitudes above 600 m above sea level as well as areas with a slope steeper than 5 %. For some areas, we added buffer zones to the exclusion areas with varying buffer distances depending on the land cover type (see Technical Annex for details and data sources). We continued with the definition of the three habitat types by means of the [Digital Landscape Model \(2010\)](#) (DLM). All arable and grassland areas of the DLM that did not overlap with the exclusion areas were classified accordingly.

We identified optimal habitats by combining further information. For optimal habitats, we assumed conditions that allow the maintenance of a high lapwing population density and good breeding success, such as wet soils, good food supply, low disturbance and vegetation that does not grow too quickly during the breeding season. Furthermore, existing

conservation measures, such as bird protection areas, nature conservation support and advisory services, are often concentrated in these areas. Thus, we defined wet soils (DLM object types peatland and marsh) and wetlands of the RAMSAR Convention (as of 2013) as well as special protection areas according to the Natura 2000 directive (SPA, as of 2014) as potential optimal habitats, as long as those sites were not yet occupied by exclusion areas or arable land or grassland, respectively. In addition, we consulted national lapwing experts to collect information on important optimal habitat areas on a regional scale and added those that were not yet covered by our own definition. In the absence of better data, this approach represents a first approximation. It is likely that we overestimated the area of optimal habitats, as, for example, not every bird protection area has the lapwing as a target species.

**3.1.1.2. Capacity limit and initial population.** For the cellular automaton, each cell needs a maximum possible population capacity per habitat type. In the absence of specific data, we used data on mean breeding pair density per ha per habitat type and multiplied them with the available habitat area per cell. Mean breeding pair density reflects the mean number of observed breeding pairs per ha in colonised habitats. We approached the maximum population capacity by applying the breeding pair density, which was only observed in populated areas, to the entire habitat area. We thus assume a homogenous distribution of lapwing breeding pairs throughout the habitat area, whereas in reality, many areas are not colonised at all, partly because of poor breeding conditions. The capacity limits that we calculated are underestimated in some cells. They are adjusted in the calibration process (cf. Technical Annex).

Data on breeding pair densities are based on the literature ([Glutz von Blotzheim, Dirksen, Niethammer, & Bauer, 1999](#); [Hegemann, Salm, & Beckers, 2008](#)) and expert knowledge (personal communication with Hermann Hötter<sup>1</sup>). Breeding pair density is smaller in habitat types with lower habitat quality; i.e., a single breeding pair needs a larger territory to fulfil all of its needs. Consequently, the breeding pair density is lower in habitat types with poor quality (arable land: 0.034 pairs per ha, followed by grassland: 0.076 pairs per ha) than in optimal habitats (0.225 pairs per ha).

The population model starts with an initial population per cell. Data for the initial population are based on the Atlas of German Breeding Bird Species (ADEBAR) ([Gedeon et al., 2014](#)), providing observation data (breeding pairs) that were recorded from 2005 to 2009. We set the start year in the population model to 2006. ADEBAR does not provide any information on the habitat of the breeding pairs for the grid cells. For this reason, we applied in the model a vague prior and allocated the initial population to the three habitat types in proportion to habitat availability in the respective grid cell.

##### 3.1.2. Parameters of the reproduction and dispersal model

**3.1.2.1. Estimates from the literature.** Input data of the reproduction model originate mainly from [Plard et al. \(2019\)](#) based on an integrated population model and observations. They include demographic parameters such as survival rate (0.77 for adult birds, 0.54 for first-year birds) and breeding probability of females (0.94 for adult birds, 0.98 for first-year birds). However, breeding success in the agricultural landscape is not from [Plard et al. \(2019\)](#), as the authors do not provide the respective data. Their values on breeding success are derived from other values. Instead, we refer to [Roodbergen et al. \(2012\)](#), who summarise available data from observation studies in Western Europe. From 1996 to 2006, the mean reproductive output of 160 studies was 0.4 fledglings per breeding pair. To determine the breeding success in optimal habitat, we

<sup>1</sup> Mr. Hötter was head of Michael Otto Institute of the German Nature and Biodiversity Conservation Union (NABU e. V.) and one of the most renowned ornithologists and scientists in the field of applied farmland bird conservation in Germany.

examined data from six reports of lapwing conservation projects in Germany, where the mean of 13 projects is 1.4 (cf. Technical Annex).

**3.1.2.2. Data from field trials.** To assess the impact of the lapwing plot conservation measure, we needed corresponding breeding success data. Therefore, we carried out field trials on arable land in different German regions (Mecklenburg-Western Pomerania, Münsterland, periphery of Brunswick in Lower Saxony, Donaumoos, Saxony, Schleswig-Holstein). The implemented lapwing plots were 0.5 to 1.8 ha sections within otherwise normally cultivated fields. During the breeding season, these sections remained fallow or were sparsely sown with a grass-clover mixture to prevent the establishment of unwanted weeds. Since lapwings also tend to build nests in the field surrounding the designated lapwing plots if the crop is suitable (i.e., offering bare soil, low and sparse vegetation at the beginning of the breeding season such as maize, sugar beet, spring-sown cereals, etc.), these nests are additionally marked so that farmers can drive around them when carrying out agricultural practices. In total, we implemented 60 lapwing plots. The plots and their surrounding area provided breeding sites for 132 pairs (including some plots with no pairs). The mean value of the breeding success for lapwing plots in summer crops was 0.77.

**3.1.2.3. Parameters derived from calibration.** The dispersal model includes the simulation of birds moving between different cells and different types of habitat in consecutive years. To model the movements between different types of habitat, we used a parameter we labelled own-habitat preference (OHP), which describes the probability that a bird breeds in the same habitat type in season  $t$  as in season  $t-1$ . A value of 1 implies that all lapwings in the present year nest in the same habitat type as in the previous year. A value of 0 means that the distribution of lapwings in the present year perfectly corresponds to the habitat availability in the present year and that there is no direct link to the lapwing distribution in the previous year. Due to a lack of data, we estimated the respective values for OHP for arable land and grassland (0.80) and optimal habitat (0.83) in the calibration process (cf. Section 3.2.3).

### 3.1.3. Parameters for cost calculation of the lapwing plot

We derived the costs for the lapwing plots based on the difference in gross margin losses between cultivating common crops and implementing lapwing plots. Gross margins differ depending on the region and the crop. We took corresponding values (crop-specific average per region) from the standard gross margins per ha (Kuratorium für Technik und Bauwesen in der Landwirtschaft e.V., 2020) and overlaid them with our grid cells and the respective average area shares of the different crops on the municipality level (Neuenfeldt, Gocht, & Röder, 2020). We focused on sugar beet, silage maize and grain maize fields, as these crops are by far the most suitable common crops for setting up lapwing plots. We therefore calculated a weighted average gross margin (WAGM) of the standard gross margins of these three crops per cell. Weighting depends on the average number of hectares cultivated with each crop in each cell.

For cost calculation, we further needed data on the required number of ha for the lapwing plot. We derived this information from the field trials that we carried out (cf. Section 3.1.2.2), where, on average, each pair needed 0.4 ha.

## 3.2. Model description

The population model simulates reproduction as well as dispersal processes between cells and types of habitat over a period of 50 years

starting in 2006. The first year in the model, as the entry into the simulation, is programmed differently from the other years. The first-year simulation is explained in the Technical Annex. The description given here starts with the regular processes from year two onwards.

### 3.2.1. Dispersal

The second year and the following years in the simulation begin with movements between cells by means of the cellular automaton. Figuratively speaking, lapwings arrive in Germany at the beginning of the breeding season and look for a suitable cell for breeding. Each cell comprises a population in a certain year, differentiated by three habitat types and two age cohorts, i.e., adult birds and first-year birds, that fledged the year before. Each habitat type in each cell is characterised by a maximum possible population capacity.

Movements are simulated for each habitat and each age cohort by a rule-based process of comparisons between cells. Emigration and immigration of birds outside Germany are neglected because we assume that the influence is low due to the lapwings' site fidelity (Imboden, 1974; Lislevand, Byrkjedal, & Grønstøl, 2009; Sharpe, Clark, & Leech, 2008; Thompson, Baines, Coulson, & Longrigg, 1994). The model simulates colony formation; i.e., lapwings move into cells with a higher population than their own cell. This refers to the observation that lapwings breed mainly in groups, as important predators (aerial predators) can be better avoided in this way (Shrubbs, 2009). Only for optimal habitats did we assume strong site fidelity so that lapwings did not move into other cells.

However, an exception exists for all habitats if the population of a cell is at least 90 % of its capacity limit and movements out of the cell are simulated to avoid overcrowding. This approach reflects the increasing competition between birds when the capacity limit is nearly reached.

In the following step, movements between habitat types within cells are computed, again separately for each age cohort. This process is mainly determined by the OHP. The number of birds leaving a certain habitat depends on the current number of birds in that habitat type and the OHP of that habitat type.

### 3.2.2. Survival and reproduction

At this point in the process, birds have found their cell and habitat, and in the next step, the model simulates survival and reproduction (Fig. 1).

First, the population at the beginning of breeding season  $t$  is determined in each cell and each habitat type. Adult birds in season  $t$  comprise adult birds from season  $t-1$  and first-year birds from season  $t-1$  multiplied by the survival rate for adult birds. The population also includes first-year birds of season  $t$ , which are fledglings from season  $t-1$  multiplied by the survival rate for first-year birds.

In the next step, the number of fledglings is determined. The number of adult birds is divided by two to form pairs and then multiplied by the breeding probability for adult birds. The process for first-year birds is similar. Both population components are then added and multiplied by the breeding success of the respective habitat. Finally, the three population components are summed up.

When simulating conservation measures, we increased breeding success values in the reproduction process. The level of breeding success depends on the assumptions made on the scale of implementation of conservation measures. For example, if 60 % of the lapwing population is protected by lapwing plots, the average breeding success in arable land is 0.62. This results in a breeding success of 0.77 for the lapwing plots and 0.40 for normal arable land ( $0.62 = 0.60 * 0.77 + 0.40 * 0.40$ ).



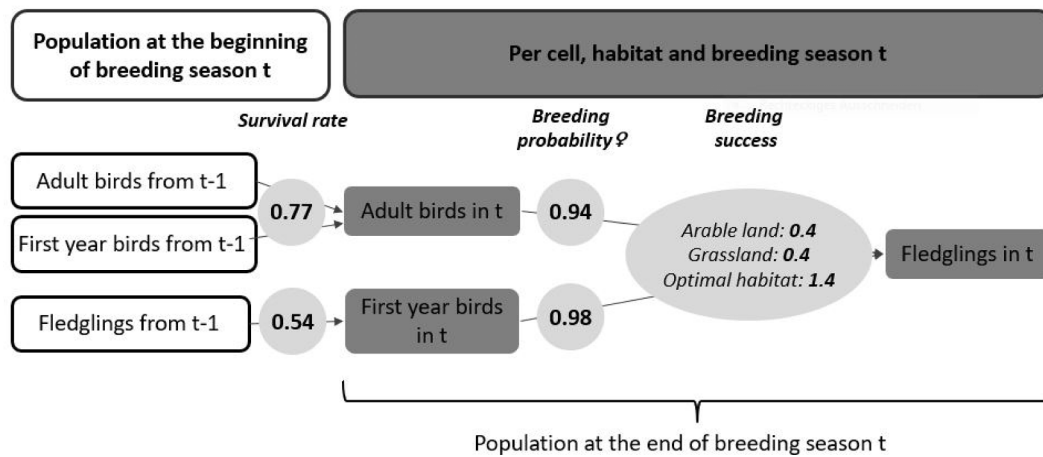


Fig. 1. Schematic representation of survival and reproduction from year two onwards (Source: own depiction based on Plard et al., 2019).

### 3.2.3. Calibration of the model

The aim of the model is to simulate population development so that it sufficiently corresponds to real development. To ensure this correspondence, we compared our simulation with estimated population levels from 1991 to 2013 based on indices by Busch et al. (2020) and population data from the German federal states. The description of how we estimated the population levels is given in the Technical Annex. The estimated populations represent three German regions (northwestern (NW), southwestern (SW) and eastern (E) Germany) that are differentiated by the spatial structures of agricultural landscapes and geographic heterogeneity (Busch et al., 2020; Sudfeldt et al., 2012).

Estimated populations refer to population development from 1991 to 2013, but the start year in our simulation is 2006 based on ADEBAR data (Gedeon et al., 2014). To generate a common starting point for the estimated population and the simulation, we set a new initial population in the model. In each cell, we multiplied the initial population (ADEBAR data) with region-specific index values for 1991 based on the indices by Busch et al. (2020) so that we were able to compare the simulated population development from 1991 to 2013 with the estimated population.

The simulation is based on input data from different sources explained in Section 3.1, including calibrated values for OHP. We used OHP for calibration, as empirical data are not available. Fig. 2 shows comparisons of the estimated population and the simulation. Overall, the model is able to predict the population development over the 23-

year period for Germany in total, and it can mimic region-specific developments, although we use global parameters in the reproduction model and for OHP. The model cannot, however, mimic year-specific volatility.

For the total German population, we observe a very good match between the simulation and the estimated population, both showing a loss of 79 %, which is mainly a result of the match in northwestern Germany, which hosts more than three-quarters of the German lapwing population. Here, we observe a population loss of 81 % in the estimated population and 82 % in the simulation. In southwestern and eastern Germany, which comprise smaller population shares (each ~ 10 %), the differences between the estimated population and simulation are greater. For southwestern Germany, the simulated population loss is somewhat higher (84 %) than for the estimated population (72 %). In eastern Germany, it is the opposite; in the simulation, the population loss is only 54 % in comparison to the estimated population with a loss of 65 %. Nevertheless, the model correctly recovers the stabilisation phase beginning around 2005.

Despite the fact that we use the same parameters in all three regions, we can reproduce region-specific population developments from 1991 to 2013 for three German regions and the total German population with the calibrated model. Underlying parameters are thus calibrated for the period 1991 to 2013. They serve as parameters for our scenarios simulating potential future developments.

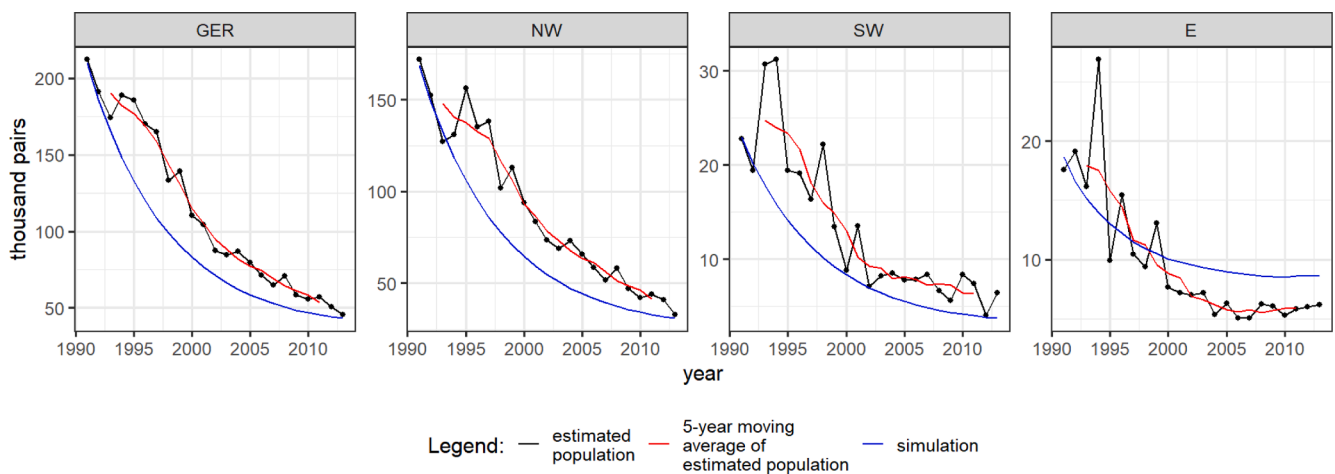


Fig. 2. Population simulation in comparison to estimated population and its five-year moving average for northern lapwing (*Vanellus vanellus*) in 1990–2013 based on the population index in Busch et al. (2020) separately for Germany in total (GER) and three German regions (northwestern Germany (NW), southwestern Germany (SW) and eastern Germany (E)).

### 3.2.4. Scenarios

**3.2.4.1. Baseline scenario with two variations.** The baseline scenario comprises a simulated population development from 2006 to 2055. This scenario shows the potential population development in the three habitat types if land use is stable and no conservation measures are taken. Furthermore, within the baseline scenario, we differentiate between a best-case and worst-case variation to account for uncertainty in our data on optimal habitat availability. We consider the best-case variation to be at the upper end of a possible range of developments. In the best-case variation, all values are included as described in the previous chapters. However, the availability of optimal habitat in our model may be overestimated, for example, because in the identified optimal habitat areas, conditions might not be as optimal as assumed for the lapwing everywhere (cf. Section 3.1.1.1). As the optimal habitat population could be overestimated in the best-case variation, we additionally set up a worst-case variation, which we consider to be the lower end of a range of possible developments without conservation measures. In this variation, we limit the capacity in the optimal habitat to the best-case simulated optimal habitat population of 2021.

**3.2.4.2. Conservation measure scenarios including cost calculation.** In five conservation measure scenarios, we simulated that different population shares between 20 % and 100 % are protected by measures from 2021 onwards, referring to both arable land and grassland. Thus, we assumed that in arable land, lapwing plots are implemented, and a similarly effective measure is implemented in grassland. Conservation measure scenarios include best-case and worst-case variations under the same conditions as in the baseline scenario.

The cost calculation refers only to lapwing plots on arable land. In each cell, the number of birds was divided by two to form pairs and then multiplied by the share of protected pairs, as costs incur only for these pairs. Then, the required hectares of lapwing plots were determined by multiplying the number of protected pairs by 0.4 ha, which is the average requirement per pair (cf. Section 3.1.3). Finally, the required hectares per cell were multiplied by the cell-specific WAGM, and the results were summed over all cells, resulting in total costs per year for Germany.

## 4. Results

### 4.1. Baseline scenario

#### 4.1.1. Population developments

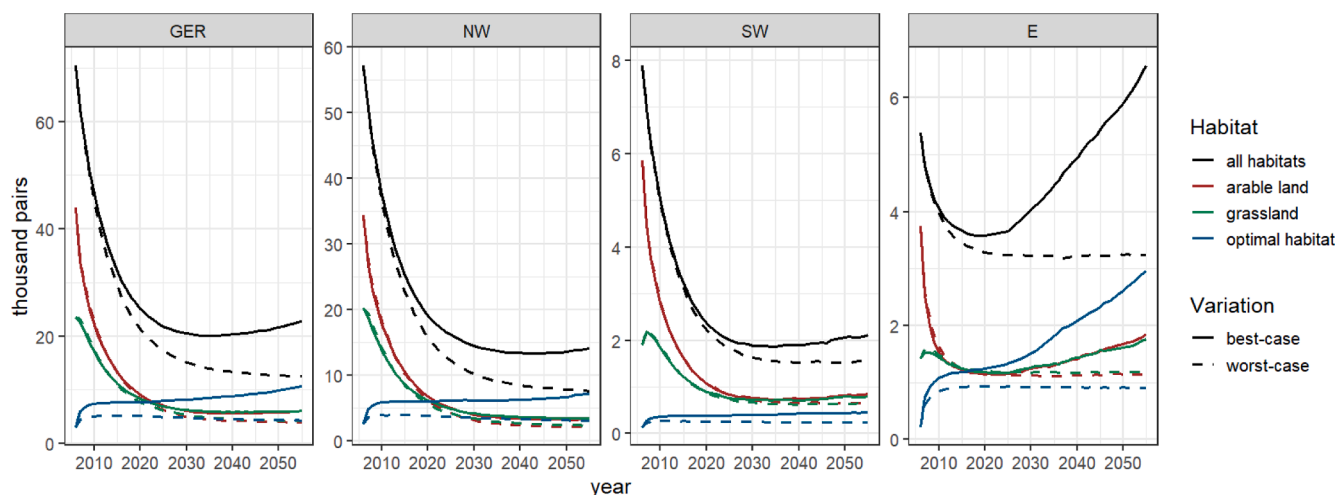
For the total German population (GER, all habitats), we observe a sharp decrease from 2006 to approximately 2020 in the best-case variation (solid line) of the baseline scenario (Fig. 3). The population stabilises in the 2030s at approximately 20 000 pairs and slightly increases from the 2040s (2055: 23 000 pairs). Populations in arable land (brown line) and grassland (green line) decrease sharply and stabilise from the 2030s at approximately 6 000 pairs per habitat. The population in the optimal habitat (blue line), however, increases until 2011, when a plateau is reached at 7 600 pairs. From 2023, the increase intensifies again so that the population is increasingly concentrated in optimal habitat. The stabilisation and slight recovery of the overall population is therefore mainly due to the population increase in optimal habitats. When optimal habitats have a considerably higher occupation than the surrounding arable land and grassland habitats, we observe movements into arable land and grassland.

In northwestern and southwestern Germany, the trends are comparable to that in Germany as a whole, except that in southwestern Germany, the population in the optimal habitat remains stable after an initial increase and is consistently lower than in the other two types of habitat. In the eastern region, however, there is a strong increase in the optimal habitat population from the 2020s. This causes not only an overall population increase but also an increase in the other two habitat types based on dispersal processes.

In the worst-case variation (dashed line), the population curve for all of Germany (GER, all habitats) flattens out strongly, i.e., the decline is slowed down considerably, but the population continues to decline until the end of the simulation (2055: 12 000 pairs). Furthermore, we observe an equilibrium between the populations in the three habitat types from 2030 onwards (approximately 4 000 pairs per habitat). In the northwestern region, the trends are comparable to those for all of Germany. In southwestern and eastern Germany, however, the populations stabilise at the end of the simulation timeline and do not continue to decline.

#### 4.1.2. Population distribution

Fig. 4 shows the population distribution for the initial population in 2006 according to ADEBAR and for the simulated years 2021 and 2055 in the worst-case variation. Distribution is depicted by the number of



**Fig. 3.** Baseline scenario (best-case and worst-case variation), separately for Germany in total (GER) and three German regions (northwestern Germany (NW), southwestern Germany (SW), eastern Germany (E)).

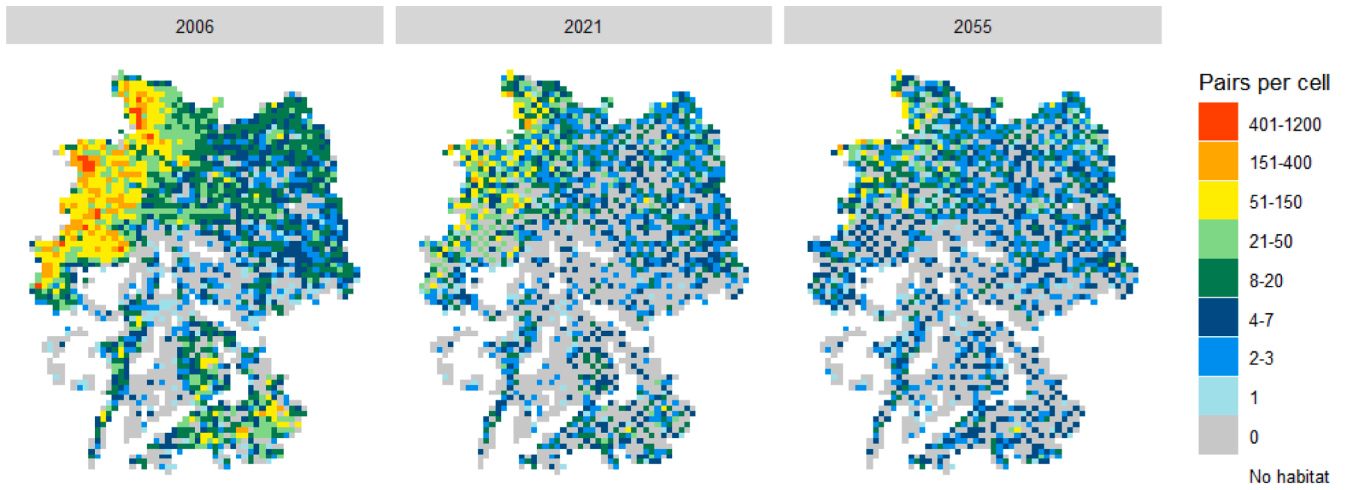


Fig. 4. Population distribution for the initial population in 2006 and potential distribution in the worst-case variation of the baseline scenario for the simulated years 2021 and 2055.

breeding pairs per cell in different frequency classes. The results for the best-case variation and for other simulated years are given in the supplementary material (Appendix B, Figure B 1 & Figure B 2).

The initial situation in 2006 shows a large population in north-western Germany with some clusters, i.e., cells more densely populated than the surrounding cells. These clusters comprise 151 to 1 200 pairs per cell (illustrated in orange and red). Particularly in the clusters, the population declines sharply in the following years. However, overall, most cells remain occupied in northwestern Germany. In 2006, in the eastern region, the population is low but evenly spread, with many cells of 8 to 20 pairs (dark green), whereas in southwestern Germany, many cells have very few or no pairs, although suitable habitat is available. Until 2021, we observe a considerable decline in eastern and southwestern Germany with more abandoned cells. Thereafter, the distribution remains largely stable.

#### 4.2. Conservation measure scenarios

##### 4.2.1. Population developments

Fig. 5 displays the development for the German lapwing population in the baseline scenario for the best- and worst-case variations and if different population shares are protected by conservation measures from 2021 onwards. The results for the different regions are in the supplementary material (Figure B 3, Figure B 4).

In the best-case variation, a protected population share of 40 % from 2021 leads to immediate population stabilisation. At this protection level, the average breeding success across all habitats is 0.8 (in 2022). In the worst-case variation, a 60 % share of protected pairs is necessary to stabilise the population. Here, the average breeding success across all habitats is 0.77 (in 2022).

##### 4.2.2. Population distribution

Fig. 6 shows the population distribution with conservation measures for the simulated year 2055 in the worst-case variation at 20 %, 60 % and 100 % protection level scenarios.

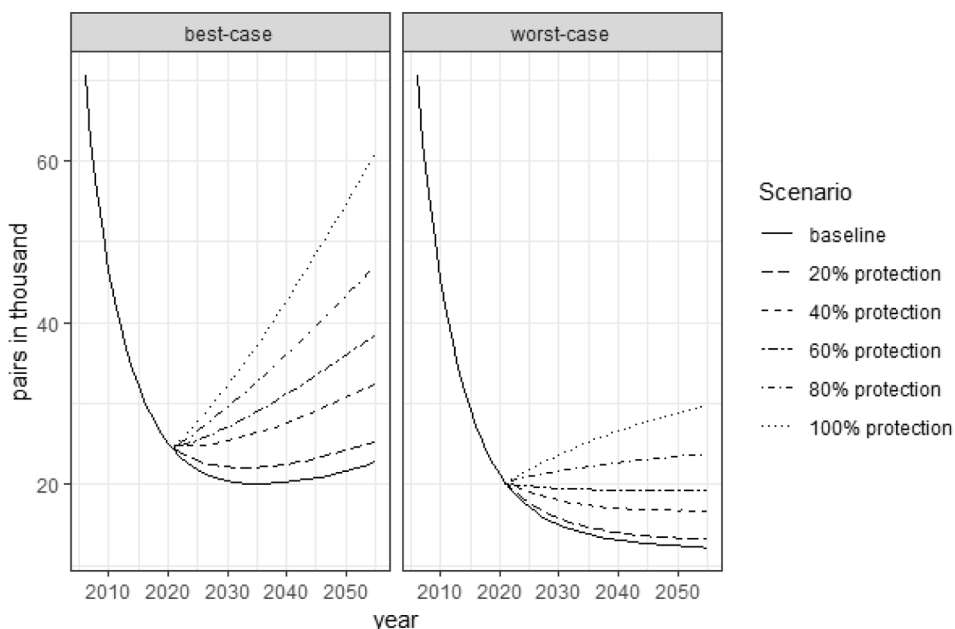


Fig. 5. Population development for Germany in total (GER) in the baseline and different protection scenarios for the best-case und worst-case variations.

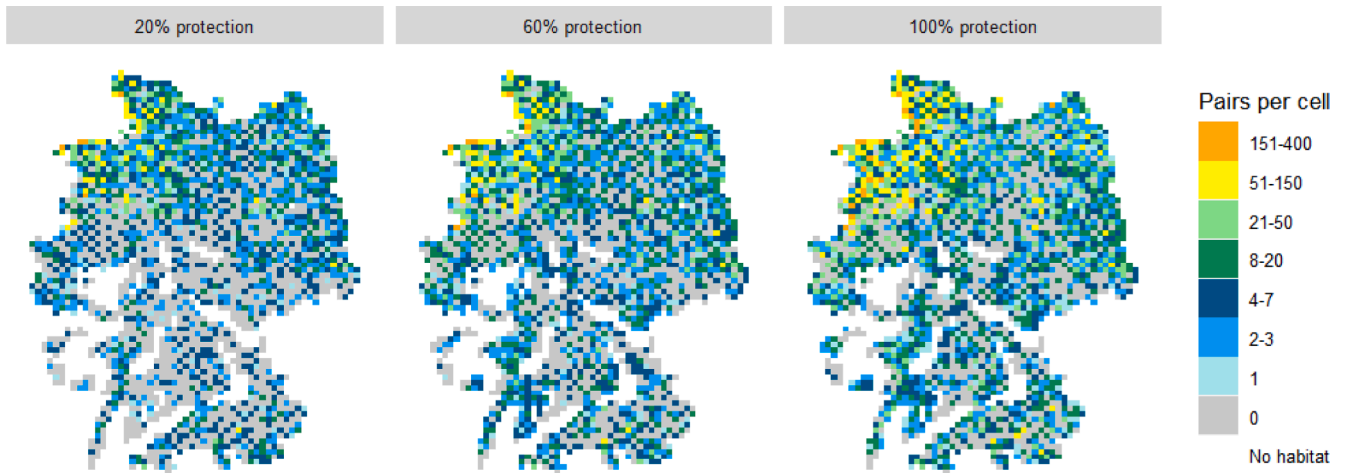


Fig. 6. Population distribution in 2055 in the worst-case variation for different protection scenarios.

In northwestern Germany, most cells are occupied in all three scenarios, but in the 60 % and especially in the 100 % scenarios, there are considerably more cells with 51 to 150 and 151 to 400 pairs. In the southwestern and eastern regions, it is particularly noticeable that in the 20 % scenario, almost no cell contains more than 20 pairs, and many cells are abandoned. In the more ambitious scenarios, we observe more clusters with 21 to 150 pairs, especially in the eastern region.

The results for other simulated protection levels (Figure B 7) and for the best-case variation (Figure B 5) are given in the [supplementary material](#). [Figure B 6](#) and [Figure B 8](#) in the [supplementary material](#) compare the spatial distribution between the baseline and different protection scenarios. In some cells, the number of pairs in the protection scenarios is lower than in the baseline scenario. This caused by the random nature of the dispersal processes.

#### 4.2.3. Required hectares and costs

Calculations for required hectares and corresponding costs refer to lapwing plots on arable land in the 60 % protection scenario, which we consider to be the minimum necessary protection level because even in the worst-case variation, it leads to population stabilisation.

In the worst-case variation, the required number of hectares at first decreases from 1 900 to 1 800 ha per year, and then the number stabilises ([Fig. 7](#)). This is because in the 60 % protection scenario, the population initially decreases, and thus the number of lapwing plots required to reach 60 % of the population decreases simultaneously. The corresponding costs are between 1.6 and 1.8 million € per year. In the best-case variation, the population almost continuously increases so that required number of hectares and costs also almost continuously increase; they range from 2 100 to 3 200 ha and 2 to 2.8 million € per year, respectively.

We further ensured that per cell, an unrealistic amount of sugar beet,

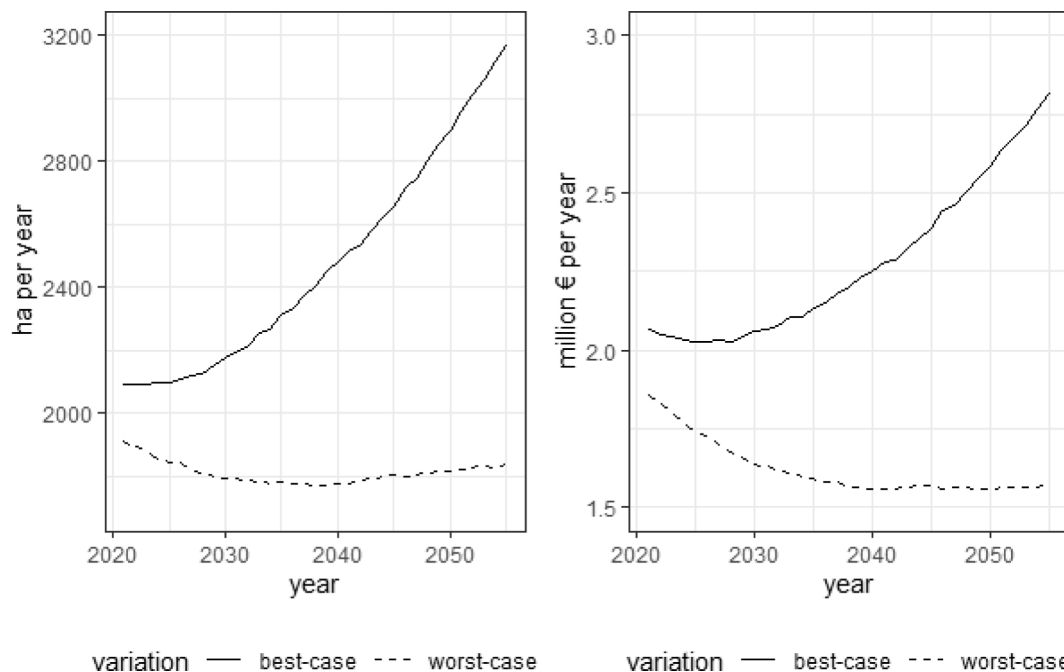


Fig. 7. Required hectares (left) and costs (right) for lapwing plots in the 60% protection scenario in the best-case and worst-case variations.



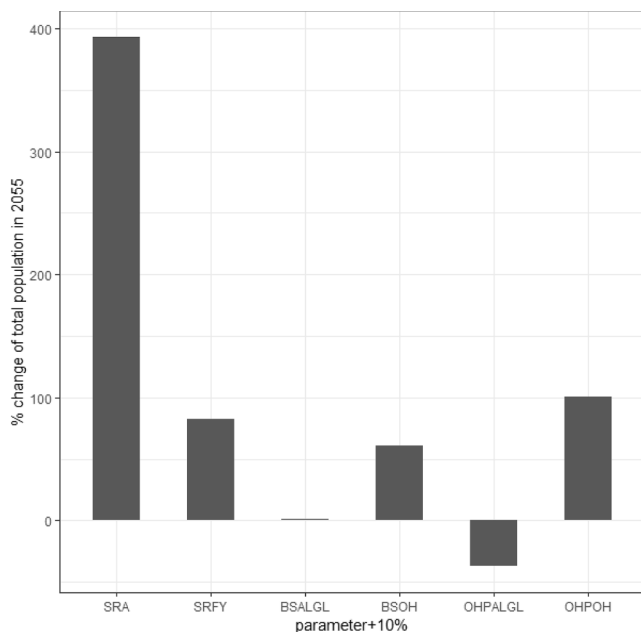
silage and grain maize fields is not required for lapwing plots. We consider a requirement of more than 10 % of these fields to be unrealistic and not practicable. For the 60 % protection scenario (best-case), in only 67 out of the 2 405 cells with suitable breeding habitat on arable land (cf. Fig. A2 Technical Annex) is this threshold exceeded (3 % of the respective cells). In the hypothetical 100 % protection scenario (best-case), this threshold is exceeded in 119 out of the 2 405 cells with suitable arable land (5 %).

#### 4.3. Sensitivity analysis

Parameters of the model are subject to uncertainty. Therefore, we performed a sensitivity analysis on the impact of possible parameter changes on the population level at the end of the simulation in 2055 in the baseline scenario (best-case variation) (Fig. 8). In the best-case variation parameter changes are more pronounced than in the worst-case variation. To be able to compare the influence of the parameters, we have increased them all by 10 %, even though a 10 % increase in some parameters are a rather theoretical scenario.

If one were to theoretically increase the adult survival rate by 10 %, the population at the end of the simulation increases by almost 400 %. The large impact can be explained by the fact that a 10 % increase in the adult survival rate means a 50 % increase in life expectancy. The impact of the survival rate of first year birds is much smaller - a 10 % increase only leads to a population increase of about 80 %. Here, life expectancy increases by only 17 %.

With regard to the impact of breeding success, there are considerable differences between habitats. In optimal habitat, 10 % increase leads to a population increase of 60 % whereas in arable land and grassland the impact is comparably marginal with about 2 %. For the distribution parameter own-habitat preference, we observe a 40 % decrease in population if the own-habitat preference for arable and grassland increases by 10 %. This is because more birds migrate into arable and grassland with a lower breeding success than in optimal habitat. An increase in the own-habitat preference of 10 % for optimal habitats however results in doubling the population.



**Fig. 8.** Sensitivity analysis. Percentage change of the simulated total population in 2055 in the baseline scenario (best-case) if different parameters increase by 10 percent: SRA = survival rate: adult birds, SRFY = survival rate: first year birds, BSALGL = breeding success arable land and grassland, BSOH = breeding success optimal habitat, OHPALGL = own habitat preference arable land and grassland, OHPOH = own habitat preference optimal habitat.

## 5. Discussion

In this study, we performed a temporally and spatially explicit population viability analysis for the northern lapwing (*Vanellus vanellus*). With the calibration, we were able to mimic past population developments for the German population and for the northwestern region comprising more than three-quarters of the German lapwing population. For the southwestern and eastern regions, the model overestimated and underestimated the population loss by 11 and 12 percentage points, respectively. This may be for several reasons. First, each of the two regions only comprises approximately 10 % of the German population. In small populations, local changes can occur that a nationwide model is not able to cover, such as changes in predation or land use. In particular, land use changed significantly in the eastern region from 1991 to 2013 due to the German reunification. Second, most parameters of the reproduction model originate from Plard et al. (2019) based on observations of the Dutch lapwing population. Most regions populated with lapwings in northwestern Germany are comparable with the Netherlands regarding spatial landscape structures and the ‘Atlantic lowland’ landscape type. However, this is not necessarily true in the eastern region, with larger spatial structures and the ‘Continental lowland’ landscape type, and in southwestern Germany, which is characterised by low mountain ranges (Busch et al., 2020; Sudfeldt et al., 2012). Third, we assume that the availability of optimal habitat tends to be overestimated in our model. This may have caused the overestimation of the population development in the eastern region in the baseline scenario. We have taken this into account by defining a baseline scenario as a best-case variation and contrasting it with a worst-case variation with a limited population breeding in optimal habitat.

Other model caveats are mainly the result of a lack of input data. First, because of the lack of habitat information, the initial population is allocated to the three habitat types in proportion to habitat availability. Consequently, the population in the optimal habitat is probably underestimated until it reaches a preliminary equilibrium after approximately four years. This means that the average breeding success across all habitats is also underestimated and that the population loss is probably overestimated in the first simulation years.

Second, dispersal processes between habitat types are determined by both the capacity limits of the habitat types in the cells and by own-habitat preferences (OHPs). Capacity limit data are based on breeding pair densities that we estimated. These estimates can be compared with results from Silva-Monteiro, Pehlak, Fokker, Kingma, and Kleijn (2021), who researched wader breeding densities as a function of land use intensity in a meta-analysis of Europe-wide data from grey literature and articles published in peer-reviewed journals. Silva-Monteiro et al.’s medium land-use intensity class corresponds to our definition of optimal habitats (low-input grassland, nature reserves specifically managed for breeding waders), and the results for northern lapwing breeding density are similar (0.22 pairs per ha) to our results. Breeding density for high land-use intensity, however, remains high in Silva-Monteiro et al. (~0.23 pairs per ha for arable land and grassland), whereas we estimate lower breeding densities for those habitats. Silva-Monteiro et al., however, critically discuss that their data are mainly from 1985 to 2005 and that since then, the population has declined drastically, especially in intensive farmland. However, even if the breeding densities and thus capacity limits were higher in arable land and grassland in our model, this would probably have little effect on the model results, since in arable land and grassland, the capacity limits are rarely reached.

Own-habitat preferences are determined in the calibration of the model. Thus, the distribution of the population among the habitat types is partly immanent to the model. From our point of view, the distribution is plausible, but it cannot be validated apart from experts’ judgement, as no corresponding data are available.

Third, population dispersal is determined by capacity limits and rule-based processes of the cellular automaton that reflect lapwing dispersal behaviour, such as colony formation and competition. The dispersal

patterns of both the baseline and the conservation measure scenarios cannot be validated with observational data. However, we have discussed rule-based processes and the dispersal results with ornithological experts who have years of expertise with lapwing conservation in Germany. Both processes and results were found to be generally plausible.

Overall, the simulated population development and dispersal should be interpreted as the results of what-if scenarios because of the above-mentioned lack of input data and because existing input data are subject to uncertainty. Most demographic parameters are based on statistical estimates with a range of uncertainty (Plard et al., 2019; Roodbergen et al., 2012). Breeding success data for optimal habitat are based on observations in 13 conservation projects. The sensitivity analysis for the baseline scenario (Fig. 8) shows that a 10 % increase in different parameters can have a marked impact on the outcome of the model (population level in 2055).

Future research could improve the accuracy of the results if better data on population distribution among habitats, OHP and dispersal behaviour were available. In particular, data on OHP would be valuable because they could be used to derive conservation measure strategies. In the case of very high OHP, it would make more sense to concentrate on the creation of optimal habitats because the population could build up in these habitats without moving to sink habitats. On the other hand, if OHP is low, it makes more sense to spread conservation efforts across all types of habitat. Additionally, the model could be refined by including more recent data of land use changes, such as the increase in maize cultivation for bioenergy (Busch et al., 2020), if the impact of such land use changes on demographic parameters, e.g., breeding success, were known.

Parameters regarding the lapwing plot (e.g., breeding success, size) were derived from the field trials that we carried out. The tests included 60 plots, which, to our knowledge, is the most comprehensive evaluation of lapwing plots in Germany that includes breeding success observations. Nevertheless, one should be careful when transferring the field trial results to a wider context. We supervised the management of lapwing plots (e.g., approaching and mobilising farmers, guidance in the selection of suitable areas). This may have led to a comparably high breeding success and to a high rate of occupation by lapwings (72 % on average). With a lower management intensity, more plots would probably remain unoccupied, leading to higher costs and a lower cost efficiency per fledgling. For example, in Chamberlain et al. (2009), breeding was suspected for only 25 % of the plots. The costs of 1.6 to 2.8 Mio € per year, which we estimated in our study, thus assume a high management intensity, and these management costs are not depicted in the cost calculation.

Moreover, cost calculation is based on cell-specific standard gross margins and is therefore a simplification. Farmers' individual costs usually differ. Furthermore, it should be noted that the cell-specific standard gross margins represent sector costs. However, the real governmental budget costs for an agri-environmental scheme would be higher. This is because in the funding practice the remuneration can only be differentiated regionally to a limited extent for administrative reasons. If a uniform remuneration rate is set for larger regions and the areas, i.e. cells, with a comparatively high gross margin are also to be addressed, the area-specific high gross margins must be paid in the entire region. Thus, producer rents arise in areas with lower gross margins. We also neglect further administrative costs that would be associated with the lapwing plot if put into practice in an agri-environmental scheme.

Despite the uncertainty in the input data and the model limitations, the results show the magnitude of implementation of conservation measures at which the population stabilises. We observed stabilisation in the best-case variation if 40 % of the population in arable land and grassland is safeguarded and the average breeding success across all habitats is 0.80. In the worst case, 60 % of the population in arable land and grassland needs to be covered by conservation measures such as the lapwing plot, and the average breeding success is 0.77. The results are in

line with Plard et al. (2019), where breeding success leading to population stabilisation ranges between 0.90 (for the Netherlands) and 0.76 (for Schleswig-Holstein in Germany). However, in comparison to Plard et al. (2019), we explicitly model how the total population is influenced by the population in optimal habitats, such as peatlands, marshes and special protection areas. Therefore, we explicitly estimate the breeding success in the normal agricultural landscape (arable and grassland) necessary for population stabilisation. Depending on the influence of the optimal habitat, a breeding success between 0.55 (best-case) and 0.62 (worst-case) in the normal agricultural landscape is necessary to stabilise the population.

Our results can further be compared with Kamp et al. (2021), who derived population size indices from 1990 to 2018 based on data from the Common German Bird Monitoring (1 200 sample plots). Accordingly, the German lapwing population decreased by 43 % between 2006 and 2018,<sup>2</sup> whereas in our baseline scenario, the population loss was higher, at 61 % (best-case) or 67 % (worst-case), in the same time period. The difference may be explained because our model is calibrated to the period 1990 to 2013, when losses were higher than those between 2006 and 2018. Moreover, as described above, the population loss in the first four simulation years is probably overestimated due to an underestimation of the optimal habitat population share. After these four years, the total population loss (from 2010 to 2018) is 41 % (best-case) or 47 % (worst-case). The results are thus within a plausible range when compared with Kamp et al. (2021).

## 6. Conclusion

The aim of this study was to assess German lapwing population development and dispersal and the impact of the lapwing plot conservation measure. We performed a temporally explicit population viability analysis using a cellular automaton and combined it with an economic analysis. A baseline scenario in two different variations projects the potential population development and spatial distribution of lapwings between 2006 and 2055. This scenario provided us with a basis for how the population could develop if land use remains stable and no additional conservation measures are taken. Building on this basis, conservation measure scenarios contrast how the population could develop if different percentages of the population are safeguarded by the use of lapwing plots in arable land and a comparably effective measure in grassland.

Conservation measures such as lapwing plots are typically implemented and financed as an agri-environmental scheme (AES) in the European Agricultural Fund for Rural Development (EAFRD) of the EU. Our model could be used for planning and ex ante evaluation of such an AES. In the new CAP funding period 2023–27, environmental targets should be formulated in the strategic plans of the member states (Art. 5, 6, 7, 70 (4) European Parliament and Council, 2021/2115). If we set the environmental target of population stabilisation of this indicator species, we can derive from our model that 60 % of the population in the normal agricultural landscape needs to be safeguarded as the minimum protection level. In the best case, the population would increase to 40 000 pairs in 2050. The model also provides the required number of hectares of arable land. With this information, one can estimate how many farmers would have to participate in AES to achieve the environmental target at the national and regional levels. For 60 % of breeding pairs to be covered by such schemes, the implementation level must increase markedly. Currently, only a small fraction of the agricultural land is enrolled in AESs that tackle biodiversity issues, such as fallow and field strips (Pabst, Achtermann, Langendorf, Horlitz, & Schramek, 2018; Röder et al., 2019).

Our results can further be used to estimate the costs of

<sup>2</sup> Values were kindly provided by the authors, also cf. Supplementary material of Kamp et al. (2021).

implementation strategies, for example, for the target of population stabilisation. The model provides cost calculations based on farmers' gross margin losses. These calculations can be combined with discrete choice experiments on lapwing plots (Buschmann, Narjes & Röder (under review)), where the results show that farmers have additional payment expectations depending on how AESs are designed.

The lapwing is an indicator species, as designated in the German indicator for 'Biodiversity and landscape quality' developed in the National Sustainability Strategy (German Federal Agency for Nature Conservation, 2021). In this context, a target population of 200 000 pairs was set (Achtziger, Stickroth, & Zieschank, 2004). Our results show that even if, in the best-case, all pairs were safeguarded, the population would only increase to 60 000 pairs in 2055. Thus, the conservation target cannot be ensured with measures such as the lapwing plot that are integrated into a normal agricultural landscape with degraded habitat conditions (e.g., low food availability). Additional measures are necessary, such as the extensification of agricultural land use (reduced fertiliser and pesticide use) and the expansion of biodiversity protection areas (Achtziger et al., 2004).

Our model could be extended in future research to simulate these additional strategies, for example, by extending the optimal habitat and then comparing or combining the effect with production-oriented measures, such as the lapwing plot. Extensification in the normal agricultural landscape may further be simulated by coupling our model results with agri-environmental models such as RAUMIS (Weingarten, 1995), which project the corresponding cost effects for farms. Another extension possibility is to simulate regionally differentiated strategies and to economically optimise measure implementation by focusing on regions with low gross margins.

## Appendix A. Technical Annex

### A.1. Introduction

This Technical Annex presents a method for developing a spatially and temporally explicit population model for the northern lapwing (*Vanellus vanellus*). The model is able to reproduce the past population development for different German regions between 1991 and 2013. On the basis of the past developments, one can project future scenarios if conservation measures, such as the lapwing plot, are applied and calculate the corresponding costs.

The model consists of two components: one for reproduction and one for dispersal, i.e., a change in the bird breeding location between two seasons. These changes include natal dispersal, i.e., young birds not breeding in the same location as they hatched. For the reproduction component, we transferred an existing matrix projection model for lapwing from Plard et al. (2019) into the programming language R (Version 1.4.1717, R Core Team, 2021). We extended Plard et al.'s model by differentiating population development in three different habitat types. To capture dispersal, we introduced a cellular automaton and developed our own algorithm (also in R). Consequently, the birds' spatial distribution can be simulated dynamically.

The Technical Annex is divided into two parts. It begins with Section A.2, explaining the input data that shape the cells of the cellular automaton (Section A.2.1), the parameters that determine reproduction and dispersal (Section A.2.2) and the cost calculation of the lapwing plot (Section A.2.3). Section A.3 describes the whole model: first the dispersal component (Sections A.3.1 and A.3.2) and then the reproduction processes (Section A.3.3). The first year in the model, as the entry into the simulation, is programmed differently from the following years (Section A.3.4). Section A.3.5 describes how the whole model is calibrated. Finally, we explain how we implemented the baseline and conservation measure strategies and how we calculated the corresponding costs (Section A.3.6).

### A.2. Data

#### A.2.1. Attributes of the cells

For the cellular automaton, we divided the German federal territory into 4 698 cells with a size of approximately  $10 \times 10$  km. The cells are arranged in 81 rows in the direction north to south and 58 columns from west to east and thus correspond to the grid cells of the Atlas of German Breeding Bird Species (ADEBAR) (Gedeon et al., 2014). The ADEBAR cells are based on ordnance sheets of the topographical map 1:25 000, which were transformed to a Gauss Krüger projection. Each cell has a row number  $i$  from 1 to 81 and column number  $j$  from 1 to 58.

**A.2.1.1. Habitat area.** Each cell consists of up to 3 habitat types  $h$ : arable land ( $h = 1$ ), grassland ( $h = 2$ ) and optimal habitat ( $h = 3$ ). In the first step, we estimated the available suitable habitat areas per cell and habitat type using PostGIS (Version 3.0.0). We followed the assumption that all areas are

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Acknowledgements

The authors would like to thank Prof. Dr. Christian Lippert from University of Hohenheim and Dominic Cimiotti from Michael-Otto-Institute in the Nature and Biodiversity Conservation Union (NABU) for their knowledgeable advice on the study.

We are also grateful to the Association of German Avifaunists (DDA) providing us with observation data on breeding bird populations and habitat preferences. In particular, we would like to thank the volunteer birdwatchers on whose efforts many of these observation data are based.

This study was conducted within the project "Lapwing: Conservation measures for a ground-nesting birds". It was funded between 2014 and 2020 as part of the Federal Programme for Biological Diversity by the German Federal Agency for Nature Conservation with resources from the Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection, the Federal State of Schleswig-Holstein, the Hanns R. Neumann Foundation and the project partner Nature and Biodiversity Conservation Union (NABU).

The funding sources had no involvement in the study design, collection, analysis and interpretation of data, in writing of the report and in the decision to submit the article for publication.

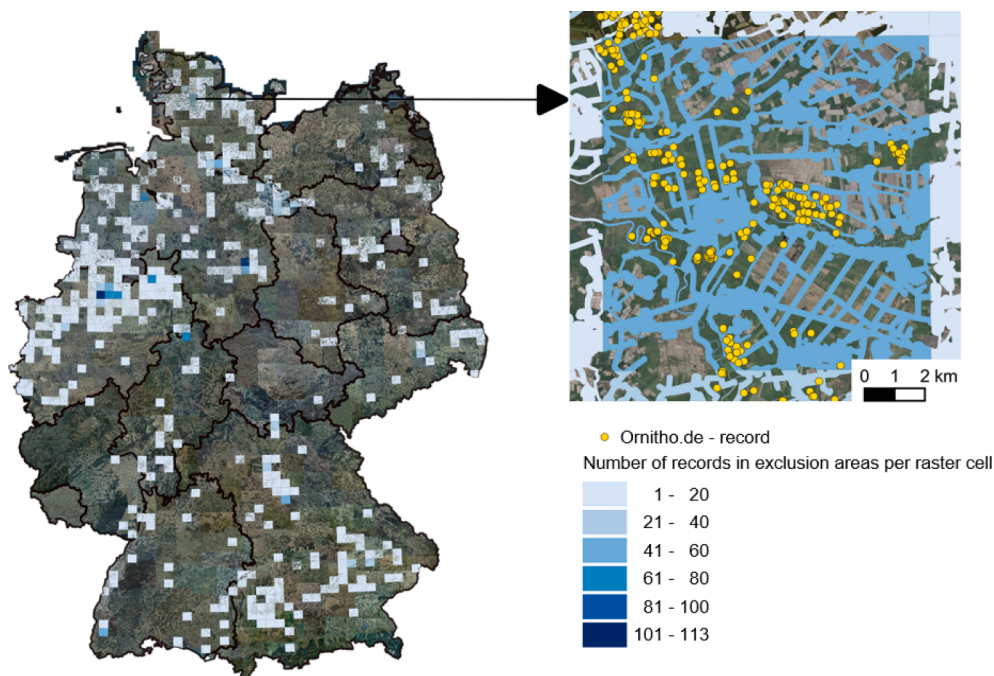
suitable as breeding habitats if they are not explicitly defined as “unsuitable” (=exclusion areas). Exclusion areas are defined by their site characteristics as follows. In some cases, they are extended by specific buffer zones (buffer distances are given in brackets):

- Natural regions that do not offer suitable areas for colonisation due to their overall characteristics according to expert assessments (e.g., low mountain range regions such as the Black Forest) and long-term absence of lapwings.
- Wooded areas/tree-covered areas (150 m buffer) and vertically rising agricultural crops such as fruit orchards and hops fields (50 m buffer).
- Transport areas such as tracks, roads, parking lots and railways (with differing buffers based on [Garniel and Mierwald \(2010\)](#)) as well as airport areas (no buffer) except for meadow areas of Munich Airport.<sup>3</sup>
- Heathland and water areas (no buffer).
- Areas at altitudes above 600 m above sea level and areas with a slope of 5 % or more, calculated on the basis of a 25 × 25 m grid throughout Germany for those grid cells not located within already excluded natural regions (see above).

The assumptions we made on the exclusion area definition are conservative. While it is likely that actually settled areas are defined as unsuitable for breeding, only a few actually nonsettled areas should be incorrectly classified as suitable. For plausibility checks and refinement of our assumptions, we used citizen science lapwing data from the webpage “[ornitho.de](#)”<sup>4</sup> for the years 2012 to 2017 ([Fig. A1](#)). A total of 63 549 data records (reports) were available, which we narrowed down to reports with a high probability of representing breeding lapwings. We only used data with the following characteristics:

- Breeding time code indicates a high probability of a nest location (at least code B6, i.e., adult bird visits a probable nest site).
- Location is classified as “exact localisation” unless an inaccuracy of more than 100 m is reported on the webpage.<sup>5</sup>

After filtering, 8 625 reports remained, with an average of four individuals. Of these reports, 6 521 were located inside or in the marginal area of the areas defined as suitable. For quality control, we checked the raster cells with a high number of outliers. The visual inspection revealed that a high number of records are just slightly within the exclusion area. This particularly concerns the buffer zone around field paths ([Fig. A1](#)). This might be because in the citizen science data, people recorded their own location and not that of observed bird, especially when using smartphones. In other cases, the presence of breeding lapwings in areas classified as being unsuitable can be attributed to some “odd” individuals, such as those breeding in, e.g., inner-city construction sites or wastelands (e.g., in Münster). Given these limitations, we regard the 75 % figure of the “[ornitho.de](#)” lapwing



**Fig. A1.** Exclusion areas (blue) and “[ornitho.de](#)” data records of northern lapwing (yellow dots; breeding time code at least B6, exact localisation, inaccuracy if indicated maximum 100 m). The depicted square (in dark blue) contains a particularly high number of “[ornitho.de](#)” reports in areas that we defined as exclusion areas (n=48).

<sup>3</sup> Munich Airport has high numbers of breeding lapwings and other meadow nesting birds between the runways. This is not known to exist in other airports in Germany.

<sup>4</sup> Application for data use no. 2017-003, data as of 27.11.2017.

<sup>5</sup> Reports of lapwing sightings transmitted to [ornitho.de](#) via a smartphone app (e.g., NaturaList) do not contain any information on accuracy. However, as these reports can be entered immediately upon observation in the field and require point location, we assume a high degree of accuracy. All “[ornitho.de](#)” points that meet the other criteria but have no indication of accuracy are therefore also included in the dataset.



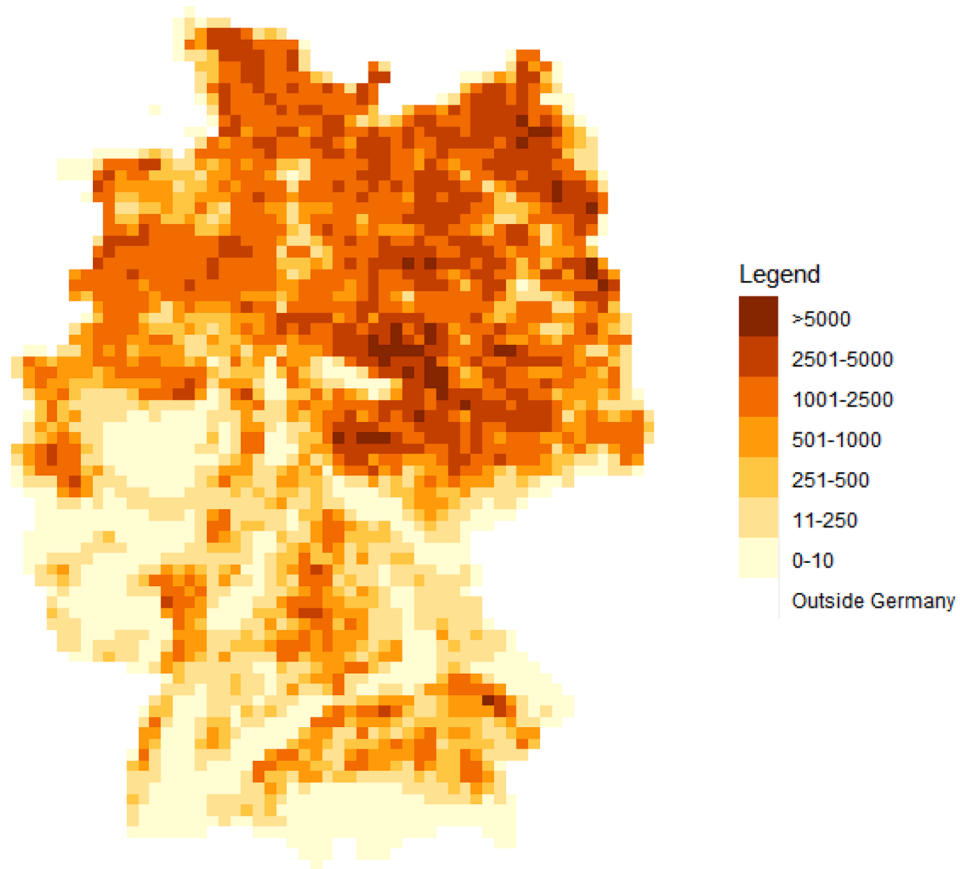


Fig. A2. Suitable breeding habitat on arable land in ha.

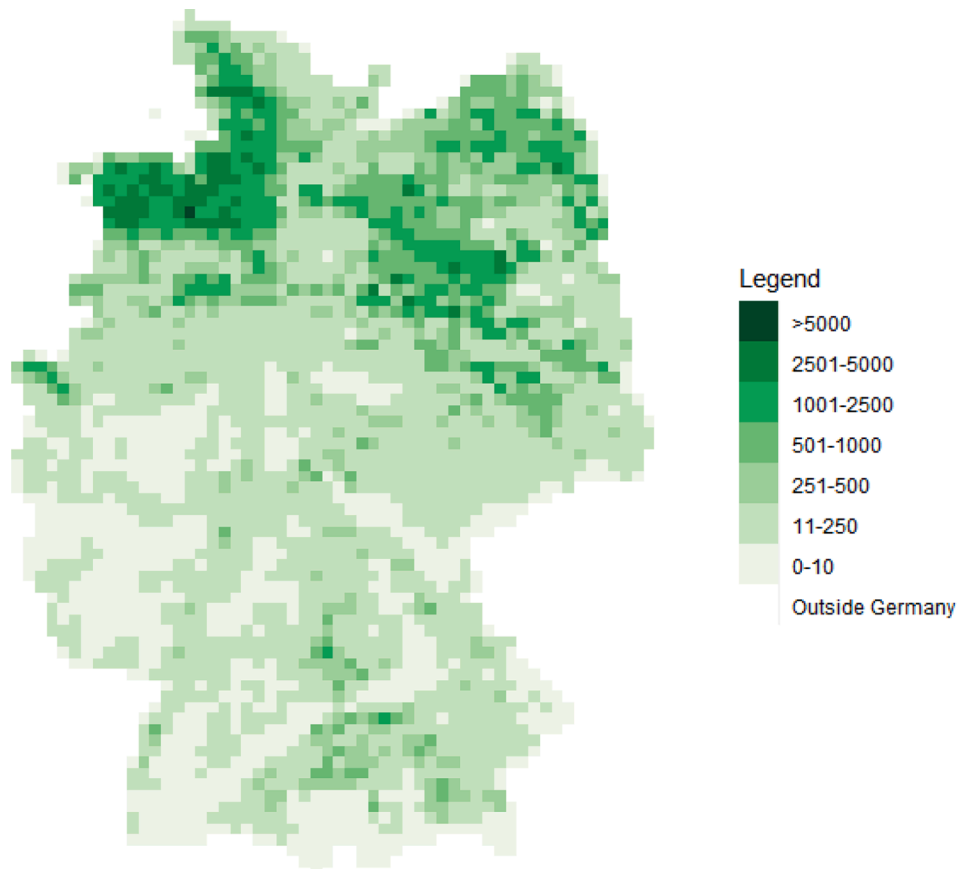


Fig. A3. Suitable breeding habitat on grassland in ha.

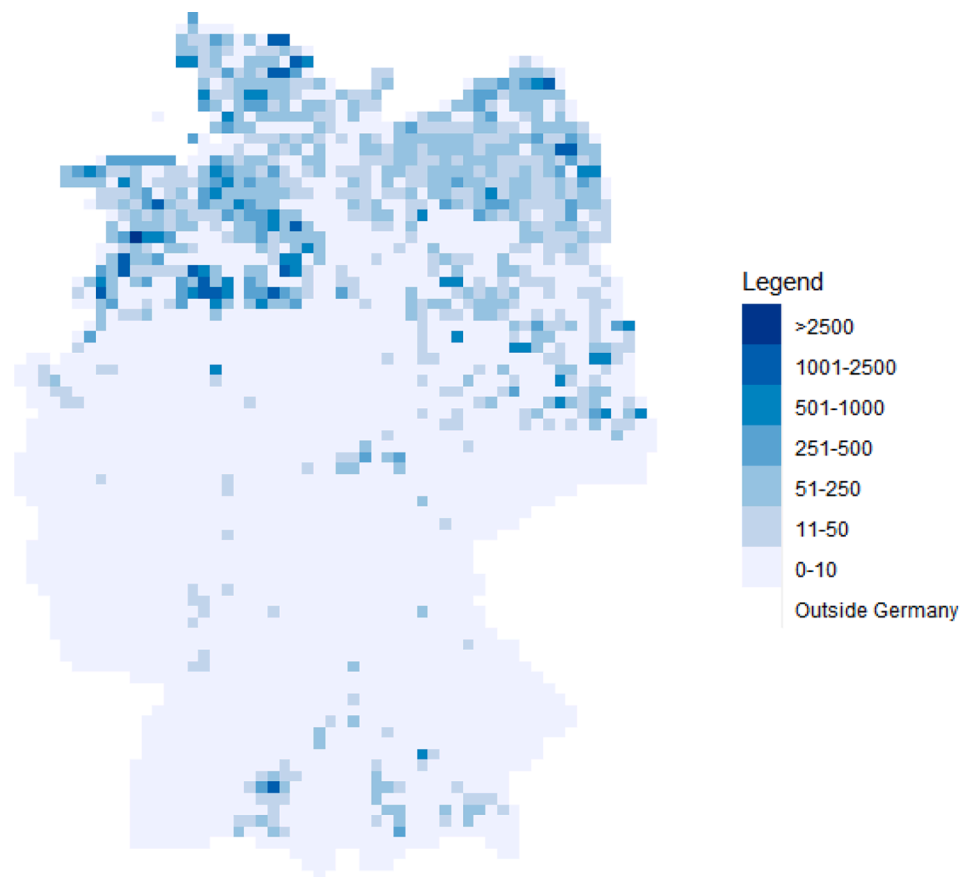


Fig. A4. Suitable optimal habitat in ha.

reports located in the areas classified to be suitable for breeding as a sufficient match and used it for further modelling steps.

We continued with the definition of the three habitat types by means of the [Digital Landscape Model \(2010\)](#) (DLM). All arable and grassland areas of the DLM that did not overlap with the exclusion areas were classified accordingly.

We identified optimal habitats by combining further information. The objective was to identify wetland habitats that offer (almost) ideal habitat characteristics for lapwings. We used the DLM to combine the object types peatland and marsh as well as special protection areas according to the Natura2000 directive (SPA, as of 2014) and wetlands of the RAMSAR Convention (as of 2013). All of these areas, which did not overlap with exclusion areas and arable land or grassland, were defined as optimal habitat. For optimal habitats, we assumed conditions that allow the maintenance of a high lapwing population density and good breeding success, such as wet soils, good food supply, low disturbance and vegetation that does not grow too quickly during the breeding season. Furthermore, existing conservation measures, such as bird protection areas and nature conservation support and advisory services, are often concentrated in areas characterised by these settings. In the absence of better data, this approach represents a first approximation. It is likely that we overestimated the area of optimal habitats, as for example, not every bird protection area has lapwing as a target species.

For the German federal territory, our analysis resulted in a total of 4.3 million hectares of land suitable as breeding habitat. Of this, 3.2 million ha are arable land (Fig. A2), 1.0 million ha are grassland (Fig. A3) and up to 0.1 million ha are optimal habitats (Fig. A4).

**A.2.1.2. Capacity limit.** For the cellular automaton, each cell needs a maximum possible population capacity per habitat type. In the absence of relevant data, we used data on mean breeding pair density per ha per habitat type and multiplied them by the available habitat area per cell. Mean breeding pair density reflects the mean number of observed breeding pairs per ha in colonised habitats. We approached the maximum population capacity by applying the breeding pair density, which was only observed in populated areas, to the entire habitat area. We thus assumed a homogenous distribution of lapwing breeding pairs throughout the entire habitat area, whereas in reality, many areas are not colonised at all, partly because of poor breeding conditions. The capacity limits that we calculated are underestimated in some cells. They are adjusted in the calibration process (cf. Section A.3.5).

Data on breeding pair densities are based on the literature ([Glutz von Blotzheim et al., 1999](#); [Hegemann et al., 2008](#)) and expert knowledge (personal communication with Hermann Hötter<sup>6</sup>). Breeding pair density is lower in habitat types with less habitat quality; i.e., a single breeding pair needs a larger territory to fulfil all its needs. Consequently, the breeding pair density is lower in habitat types with lower quality (arable land: 0.034, followed by grassland: 0.076) than in optimal habitats (0.225).

<sup>6</sup> Mr. Hötter was head of Michael Otto Institute of the German Nature and Biodiversity Conservation Union (NABU e. V.) and one of the most renowned ornithologists and scientists in the field of applied farmland bird conservation in Germany.

**Table A1**  
Parameters of the reproduction and dispersal model.

Model component	Parameter	Value	Type of source	Source
Reproduction	Survival rate: adult birds	0.77	Literature	Plard et al., 2019
	Survival rate: first-year birds	0.54		Plard et al., 2019
	Breeding probability female: adult birds	0.94	Field experiments	Plard et al., 2019
	Breeding probability female: first-year birds	0.98		Plard et al., 2019
	Breeding success (nr. of fledglings per pair and year): arable land and grassland	0.40		Roodbergen et al., 2012
	Breeding success (nr. of fledglings per pair and year): optimal habitat	1.40	Own source	Kliebe, 2002/2003; Cimiotti, 2017; Bayerisches Landesamt fuer Umwelt, 2020; Planungsgemeinschaft Marienau, 2020; Wagner, 2020; Weickelt, 2020
	Breeding success (nr. of fledglings per pair and year): lapwing plots on arable land (summer crops)	0.77		Own source
Dispersal	Own-habitat preference: arable land and grassland	0.80	Calibration	Own source
	Own-habitat preference: optimal habitat	0.83		Own source

**A.2.1.3. Initial population.** The population model starts with an initial population per cell. Data for the initial population are from the Atlas of German Breeding Bird Species (ADEBAR) (Gedeon et al., 2014), which provides observation data (breeding pairs) that were recorded from 2005 to 2009. We set the start year in the population model to 2006. In ADEBAR, population numbers are given in abundance classes with a lower and upper bound, for example, 8 to 20 breeding pairs per cell. To have one population number per cell, we determined the geometric mean ( $m$ ) between the lower ( $l$ ) and upper ( $u$ ) bounds ( $m = \sqrt{l \cdot u}$ ) to reflect the characteristics of a right-skewed lognormal distribution. As a result, the determined population number per cell is somewhat lower than the arithmetic mean of the abundance class. Since ADEBAR observations are based on breeding pairs, but the model works with the number of birds, the determined population number is multiplied by two.

ADEBAR does not provide any information on the habitat of the breeding pairs for the grid cells. For this reason, we applied in the model a vague prior and allocated the initial population to the three habitat types in proportion to habitat availability in the respective grid cell.

#### A.2.2. Parameters of the reproduction and dispersal model

The remaining parameters that serve as model input are summarised in Table A1, sorted by the model components (reproduction and dispersal) and types of sources.

**A.2.2.1. Estimates from the literature.** Demographic parameters originate mainly from Plard et al. (2019), who determine these parameters based on an integrated population model and observations from the lapwing population in the Netherlands. The study also includes data from Germany, but only from 3 sites in the federal state Schleswig-Holstein (SH) with good habitat conditions, namely, wet floodplains and marsh in a river estuary. The demographic rates resulting from these habitat conditions cannot be transferred to all of Germany. The calibration process (cf. Section A.3.5) is also not successful with these SH data.

The data from the Dutch model, on the other hand, refer to the entire Dutch lapwing population on the basis of a large dataset (approximately 28 000 ringed birds) and represent different sites and habitats. At the same time, more than three-quarters of the German lapwing population breeds in regions that are comparable with those in the Netherlands regarding spatial landscape structures and the “Atlantic lowland” landscape type. Survival rates and breeding probabilities are differentiated by age cohorts, i.e., adult birds from the 3rd calendar year onwards and birds that potentially breed in their first year (2nd calendar year). Plard et al. report breeding probabilities for both males and females. However, we applied the reported data for females to males in the model because the data on females are more reliable; females are easier to observe because they spend more time incubating eggs than males (Plard et al., 2019).

Another key parameter of the reproduction model is breeding success, i.e., the number of fledglings per pair and year, for which we distinguished between habitat types: agricultural landscape (arable land or grassland) without and with conservation measures and optimal habitat. With regard to the agricultural landscape, we did not take values from Plard et al. (2019), as the authors do not provide the respective data for the Netherlands. Their values on breeding success are derived from other values. Instead, we referred to Roodbergen et al. (2012), who summarise available data from observation studies in western Europe. From 1996 to 2006, the mean reproductive output of 160 summarised studies was 0.4. The authors emphasise that breeding success has stabilised during this period compared to previous decades.

To determine the breeding success in optimal habitat, we researched data from six reports of lapwing conservation projects in Germany. The habitats described here include wet arable land, fenced arable land, riparian margins with optimal food availability and extensively managed wet meadows. The mean breeding success of observation data in 13 projects is 1.4.

**A.2.2.2. Data from field trials.** One of the model objectives is to assess the potential impact of a conservation measure on the development and distribution of the German lapwing population. To this end, we needed the breeding success data of the conservation measure. We carried out field trials of lapwing plots on arable land in different German regions (Mecklenburg-Western Pomerania, Münsterland, periphery of Brunswick in Lower Saxony, Donaumoos, Saxony, Schleswig-Holstein). The lapwing plot is a 0.5 to 1.8 ha section of an otherwise normally cultivated field in the surrounding area. During the breeding season, the section remains fallow or is sparsely sown with a grass–clover mixture to prevent the establishment of unwanted weeds. Since lapwings also tend to build nests on the field surrounding the designated lapwing plots if the crop is suitable (i.e., offering bare soil, low and sparse vegetation at the beginning of the breeding season, such as maize, sugar beet, spring sown cereals, etc.), these nests are additionally marked so that farmers can drive around them when carrying out agricultural practices. In total, we implemented 60 lapwing plots. The plots and their vicinity provided breeding sites for 132 pairs (including some plots with no pairs). The mean value of the breeding success for lapwing plots in spring crops is 0.77.

**A.2.2.3. Parameters derived from calibration.** The dispersal model includes the simulation of birds changing between different types of habitat. For this simulation, we needed data on the so-called own-habitat preference (OHP), which describes the probability that a bird breeds in the same habitat type in season  $t$  as in season  $t-1$ . A value of 1 indicates that all lapwings in the present year nest in the same habitat type as in the previous year. A value of 0 indicates that the distribution of lapwings in the present year perfectly corresponds to the habitat availability in the present year and that there is no direct link to the lapwing distribution in the previous year. Due to a lack of data, we estimated values of 0.8 for arable land and grassland and 0.83 for optimal habitat as part of a calibration process; i.e., we varied the OHP within a reasonable range until we reached a sufficient match between the model results and estimated population levels from 1991 to 2013 based on indices by Busch et al. (2020) and population data from the German federal states. These relatively high values reflect the observation that lapwings repeatedly breed in similarly structured areas. Several studies show that the majority of lapwings (60–80 %) breed close (within 19 km) to the location in which they were hatched (site fidelity) (Imboden, 1974; Lislevand et al., 2009; Sharpe et al., 2008; Thompson et al., 1994). Site fidelity correlates with OHP because sites in proximity often have the same habitat conditions (spatial correlation).

### A.2.3. Parameters for cost calculation of the lapwing plot

The model is able to calculate the costs of implementing a conservation measure using a scenario approach. We derived the costs of implementing lapwing plots based on the gross margin losses of the farmers if they do not cultivate crops on their land but instead install a lapwing plot. Put simply, gross margin losses are the revenues minus the variable costs<sup>7</sup> that would have been incurred for cultivating the land.

Gross margins differ depending on the region and the crop. We calculated crop-specific average gross margins per region based on standard gross margins per ha (Kuratorium für Technik und Bauwesen in der Landwirtschaft e.V., 2020) and the respective average physical yields from 2014 to 2018 at the county level (DeStatis Statistisches Bundesamt). We weighted these regionalized costs with the respective average regional area shares of the suitable crops taken from Neuenfeldt et al. (2020) and overlaid them with the grid cells. To calculate the gross margin for silage maize, we derived the gross margin for the regional stock of roughage feeders (i.e., cattle, sheep, horses) and biogas production and distributed it to the main forage area (i.e., grassland, leys and silage maize) proportionally to the respective share of total roughage produced. Regarding the total area in Germany, sugar beet, silage maize and grain maize fields are the relevant crops suitable for setting up a lapwing plot. Therefore, we focused our analysis on these three crops and calculated, per cell ( $i,j$ ), a weighted average gross margin (WAGM) of the standard gross margins (SGMs) of these three crops ( $c$ ). The weighting factors depend on the average number of hectares ( $ha$ ) cultivated with each crop ( $c$ ) in each cell ( $i,j$ ).

$$WAGM_{i,j} = \frac{\sum_{c=1}^n ha_{i,j,c} * SGM_{i,j,c}}{(\sum_{c=1}^n ha_{i,j,c})} \quad (1)$$

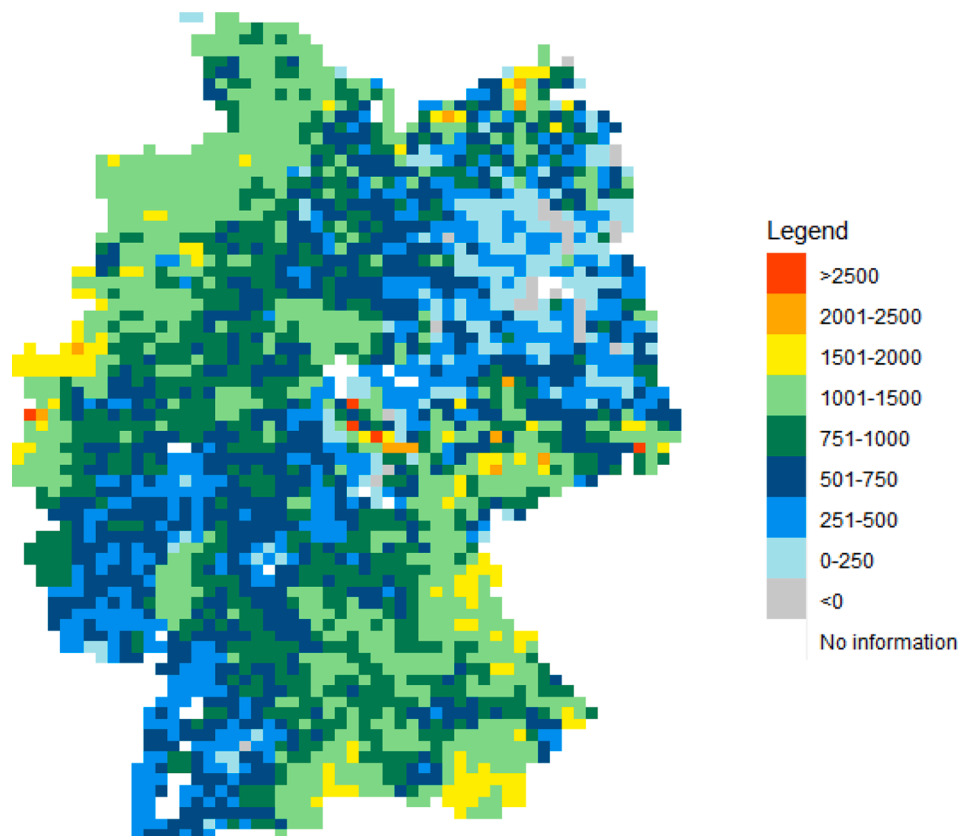


Fig. A5. Weighted average gross margin (WAGM) per ha in € (included crops: sugar beet, silage maize and grain maize, weighted per area under each crop).

<sup>7</sup> Excluding wage costs, as they are imputed costs for family farms.



Fig. A5 shows the results of these calculations for Germany. In 28 cells, we observed a negative gross margin. These cells are characterised by combinations of low densities of roughage feeders (i.e., mainly cattle) in relation to the available main forage area, a predominance of low-income animal husbandry (mainly suckler cows) and a low density of biogas plants. These combinations result on the local level in a large supply of forage on the one hand and a low demand on the other hand or a demand generating little added value. This situation is aggravated by the fact that suckler cow farming and other forms of low-input grassland management are financed to a large extent by direct payments and agri-environmental schemes (2nd pillar of the European Common Agricultural Policy). However, these payments are not included in our gross margin calculation. In addition, it is likely that a relevant share of forage is traded at the regional level (especially feedstock for biogas plants).

For cost calculation, we further needed data on the required number of ha for the lapwing plots. We derived this value from the field trials that we carried out, where, on average, each pair needed 0.45 plots or 0.4 ha (cf. Section A.2.2.2).

### A.3. Model description

The population model simulates reproduction as well as different dispersal processes over a period of 50 years starting in 2006. The first year in the model, as the entry into the simulation, is programmed differently from the other years. To provide a better understanding, the description starts with the regular processes from year two onwards. Section A.3.1 describes movements of lapwings between cells, followed by movements between types of habitat in Section A.3.2. Thereafter, Section A.3.3 explains the reproduction processes. Finally, Section A.3.4 describes the differences in the first year of the model.

#### A.3.1. Movements between cells (dispersal model)

From the second year on, the simulation begins with movements between cells by means of the cellular automaton. Figuratively speaking, lapwings arrive in Germany at the beginning of the breeding season and look for a suitable cell for breeding. This process is simulated separately for each habitat type and each age cohort. As adult birds and first-year birds differ in their reproductive behaviour, it is important to perform the calculation for both groups separately in this phase. Chicks do not move between cells. They are born in season  $t$  and then only move in season  $t + 1$  as first-year birds.

Each cell of the cellular automaton comprises a population (pop.) in season  $t$ , differentiated by 3 habitat types  $h$  and two age cohorts  $a$ , i.e., adult birds ( $a = 1$ ) and first-year birds ( $a = 2$ ).

$$pop_{i,j,h,a,t} \tag{2}$$

Furthermore, each habitat type in each cell is characterised by a maximum possible population capacity, which is calculated by multiplying the available habitat area  $ha_{i,j,h}$  and the breeding pair density per habitat type  $breeding\ pair\ density_h$ .

$$capacity_{i,j,h} = ha_{i,j,h} * breeding\ pair\ density_h \tag{3}$$

Movements are simulated by a rule-based process of comparisons between cells with suitable habitat types ( $capacity_{i,j,h}$  greater than 0) within Germany. Emigration and immigration of birds outside Germany are neglected because we assume that the influence is low due to the lapwings' site fidelity (Imboden, 1974; Lislevand et al., 2009; Sharpe et al., 2008; Thompson et al., 1994). For comparisons, the relative occupancy (in percent) per cell and habitat type for each year is decisive. We calculated occupancy by dividing the sum of adult and first-year birds by the capacity.

$$occupancy_{i,j,h,t} = \frac{\sum_{a=1}^{a=2} pop_{i,j,h,a,t}}{capacity_{i,j,h}} * 100 \tag{4}$$

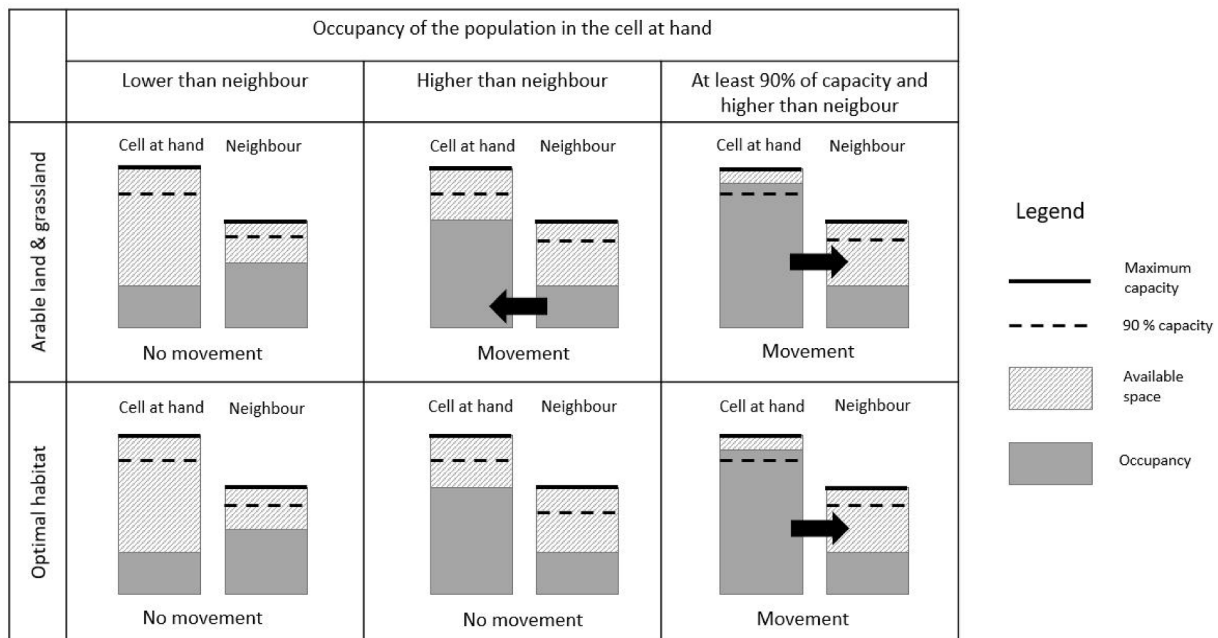


Fig. A6. Schematic representation of movements between populations of neighbouring cells for arable land and grassland (above) and optimal habitat (below), if the cell at hand ( $pop_{i,j,h,a,t}$ ) has a lower occupancy (left) or higher occupancy (middle) than the neighbouring cell ( $pop_{i+1,j,h,a,t}$ ) or when the cell at hand has an occupancy of at least 90 % and the occupancy is higher than in the neighbouring cell (right).

The occupancy of each habitat type in each cell,  $occupancy_{i,j,h,t}$ , is compared with the occupancy of a directly neighbouring cell, e.g., the right-hand cell  $occupancy_{i,j+1,h,t}$ , to determine the quantity of movement (number of lapwings) into or out of the cell at hand. The vice versa comparison occurs later, when the right-hand cell is the cell at hand and is compared with its left-hand neighbour.<sup>8</sup>

The processes distinguish between arable land and grassland on the one hand and optimum habitat on the other. In addition, a distinction is made as to whether the cell at hand is at least 90 % occupied. Fig. A6 shows the different cases, which we explain in the following.

We begin with arable land and grassland if the cell at hand is occupied by less than 90 %. In this case, the model simulates colony formation; i.e., movement takes place only from the less occupied cell to the more occupied cell. Colony simulation refers to the observation that lapwings breed mainly in groups, which is attributed to the fact that important predators (aerial predators) can be better avoided in groups (Shrubb, 2009). In the model, this means that movement does not occur if the neighbouring cell has a higher occupancy than the cell at hand (Fig. A6, above left). If, however, the neighbouring cell has a lower occupancy, movement into the population of the cell at hand is activated (Fig. A6, above middle).

The quantity of the birds moving,  $movement_{i,j+1,h,a,t}$ , depends on the degree of occupancy in the neighbouring cell. The lower the occupancy is, the more the neighbouring cell is emptied. This reflects the assumption that sparsely populated cells are characterised by poor breeding conditions and that the incentive to leave is higher than in more populated cells. Given, for example, a capacity of 1 000 birds in the neighbouring cell and actual population of 50 birds arriving in spring, the occupancy would be 5 %. In this case, we assume that 5 birds (9.5 % of 50 birds) move to the cell at hand ( $(100-occupancy_{i,j+1,h,t})/10$ ). However, if the occupancy of the neighbouring cell is 70 % (700 birds), only 21 birds (3 % of 700 birds) move to the cell at hand.

$$movement_{i,j+1,h,a,t} = \left( \frac{100 - occupancy_{i,j+1,h,t}}{10} \right) * pop_{i,j+1,h,a,t} \quad (5)$$

After the movement quantity is determined, it is added to the population in the cell at hand and subtracted from the population in the neighbouring cell.

$$pop_{i,j,h,a,t} = pop_{i,j,h,a,t} + movement_{i,j+1,h,a,t} \quad (6)$$

$$pop_{i,j+1,h,a,t} = pop_{i,j+1,h,a,t} - movement_{i,j+1,h,a,t} \quad (7)$$

The situation is different if, in arable land or grassland, the cell at hand cell is at least 90 % occupied. In this case, movement out of the cell is simulated to avoid overcrowding. This approach reflects the increasing competition between birds when the capacity limit is nearly reached. However, if the neighbouring cell has an even greater occupation than the cell at hand, no movement is simulated.

If the cell at hand is at least 90 % occupied and the neighbouring cell has a lower occupancy, movement is activated (Fig. A6, above right). Determination of movement quantity  $movement_{i,j,h,a,t}$  does not, in this case, follow the principle of colony formation but rather the principle of balancing bird numbers between cells. Movement quantity depends on the number of birds (adult and first-year birds) above 90 % occupancy ( $capacity * 90/100$ ).

$$movement_{i,j,h,a,t} = (pop_{i,j,h,a=1,t} + pop_{i,j,h,a=2,t}) - capacity_{i,j,h} * 90/100 \quad (8)$$

Movement quantity is subtracted from the population of the cell at hand and added to the population of the neighbouring cell, but only in one age cohort, as movement processes are simulated separately for each age cohort. For example, if a population of 20 adult birds and 5 first-year birds in the cell at hand together exceeds the 90 % capacity (19 birds) by 6 birds, then depending on whether the current movement simulation refers to adult birds ( $a = 1$ ) or first-year birds ( $a = 2$ ) (determined by random), the 6 birds are subtracted from either the population of adult birds or that of first-year birds. If the current population in the age cohort of the cell at hand is lower than the movement quantity, then the movement quantity is reduced accordingly. Thus, in our example, only 5 and not 6 birds are subtracted from the first-year birds in the cell at hand. Accordingly, 5 birds are added to the population in the neighbouring cell.

$$pop_{i,j,h,a,t} = pop_{i,j,h,a,t} - movement_{i,j,h,a,t} \quad (9)$$

$$pop_{i,j+1,h,a,t} = pop_{i,j+1,h,a,t} + movement_{i,j,h,a,t} \quad (10)$$

The processes described above (Equations (5) to (10)) are simulated for the grassland and arable land habitat types in all cells. Comparisons are made with all four directly neighbouring cells, i.e., above, below, to the right and to the left of the cell at hand. A random generator determines the order of the comparisons.

The dispersal process is simulated differently in the case of optimal habitats ( $h = 3$ ). Here, we assume strong site fidelity, so that no movement is simulated between neighbouring cells if the cell at hand is less than 90 % occupied (Fig. A6, below left and middle). From an occupancy of 90 % and higher, movement is simulated analogously to that in grassland and arable land habitat (Equations (8) to (10)) (Fig. A6, below right).

Independent of the habitat type, movement into neighbouring cells is possible only up to the capacity of the respective neighbouring cell. If the neighbouring cell does not have sufficient capacity, lapwings remain in the cell at hand. If the capacity in the cell at hand is exceeded, surplus individuals are randomly distributed to other (not neighbouring) cells that have sufficient free population capacity. Distribution is simulated across habitat types; i.e., the target habitat is determined at random.

In the final step, the whole dispersal process is repeated for the other age cohort. The order of age cohorts is again determined by a random generator.

### A.3.2. Movements between types of habitat (dispersal model)

Movements between habitat types within cells are computed in the following step, again separately for each age cohort. This process is determined based on the own-habitat preference (OHP) (cf. Section A.2.2.3). The number of birds (adult birds or first-year birds) leaving a certain habitat type (e.g.,  $h = 1$ ), i.e., movement quantity, depends on the current number of birds in that habitat type and the OHP of that habitat type.

<sup>8</sup> Although we refer to movements in geographical space, we use the language of the cellular automaton here and therefore speak, e.g., of the right-hand cell, rather than the cell to the east.

$$movement_{i,j,a,h=1,t} = pop_{i,j,a,h=1,t} * (1 - OHP_{h=1}) \tag{11}$$

Movement quantity is subtracted from the number of individuals in the habitat type at hand (e.g.,  $h = 1$ ) and added to the population of another habitat type, e.g.,  $h = 2$ , up to the capacity in that habitat type within the same cell.

$$pop_{i,j,a,h=1,t} = pop_{i,j,a,h=1,t} - movement_{i,j,a,h=1,t} \tag{12}$$

$$pop_{i,j,a,h=2,t} = pop_{i,j,a,h=2,t} + movement_{i,j,a,h=1,t} \tag{13}$$

All movements between the three habitat types were calculated according to this principle. This means that in our example, the opposite movement from  $h = 2$  to  $h = 1$  follows later. Since the order of movements influences the results (e.g., first from  $h = 1$  to  $h = 2$  and then from  $h = 2$  to  $h = 1$  or vice versa), it is determined randomly every year. Again, finally, the whole process is repeated for the other age cohort, and the order of the age cohorts is randomly generated.

### A.3.3. Survival and reproduction

At this stage in the process, birds have found their cell and habitat. In the next step, the model simulates survival and reproduction according to the scheme in Fig. A7.

First, the population at the beginning of breeding season  $t$  is determined in each cell and each habitat type. Adult birds ( $a = 1$ ) in season  $t$  comprise adult birds from season  $t-1$  and first-year birds ( $a = 2$ ) from season  $t-1$  multiplied by the survival rate for adult birds ( $SR_{a=1}$ ).<sup>9</sup>

$$pop_{i,j,h,a=1,t} = (pop_{i,j,h,a=1,t-1} + pop_{i,j,h,a=2,t-1}) * SR_{a=1} \tag{14}$$

The population also includes first-year birds ( $a = 2$ ) of season  $t$ , which are fledglings ( $a = 3$ ) from season  $t-1$  multiplied by the survival rate for first-year birds ( $SR_{a=2}$ ).

$$pop_{i,j,h,a=2,t} = pop_{i,j,h,a=3,t-1} * SR_{a=2} \tag{15}$$

In the next step, the number of fledglings  $pop_{i,j,h,a=3,t}$  is determined. To this end, the number of adult birds  $pop_{i,j,h,a=1,t}$  is divided by two to form pairs and then multiplied by the breeding probability for adult birds  $BP_{a=1}$ . Similarly, pairs of first-year birds  $pop_{i,j,h,a=2,t}$  are formed and multiplied by the breeding probability of first-year birds  $BP_{a=2}$ . Both population components are added and multiplied by the breeding success of the respective habitat type  $BS_h$ .

$$pop_{i,j,h,a=3,t} = \left( \frac{pop_{i,j,h,a=1,t} * BP_{a=1}}{2} + \frac{pop_{i,j,h,a=2,t} * BP_{a=2}}{2} \right) * BS_h \tag{16}$$

Finally, the three population components are summed up.

$$pop_{i,j,h,t} = \sum_{a=1}^{a=3} pop_{i,j,h,a,t} \tag{17}$$

Following reproduction, the whole model starts with simulation of the next season,  $t + 1$ , by modelling movements between cells. First-year birds from season  $t$  become adult birds in season  $t + 1$ . The fledglings from season  $t$  become first-year birds in season  $t + 1$ .

The aim of this work is to calculate the potential impact of the lapwing plot conservation measure. Since this measure increases breeding success, we implement the conservation measure by altering breeding success values in the reproduction process of the model. Fig. A8 shows the process including changes, if conservation measures are applied, in the box with the dashed line.

The level of breeding success depends on the assumptions made on the scale of the implementation of conservation measures. For example, in Fig. A8, we assume that 60 % of the lapwing population is protected by lapwing plots. Thus, for 60 % of the population, the breeding success is 0.77 (lapwing plot), and for the remaining 40 %, it is 0.4 (conventional arable land), resulting in an average breeding success of 0.62 ( $=0.6 * 0.77 + 0.4 * 0.4$ ) for arable land.

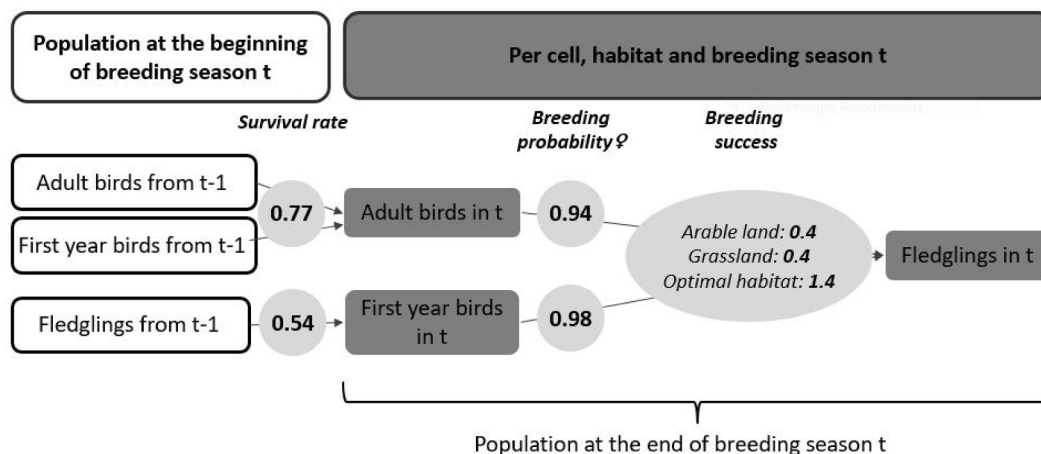


Fig. A7. Schematic representation of reproduction from year two onwards (Source: own depiction based on Plard et al. (2019)).

<sup>9</sup> In season two, there are no first-year birds from season one (cf. Section A.3.4).

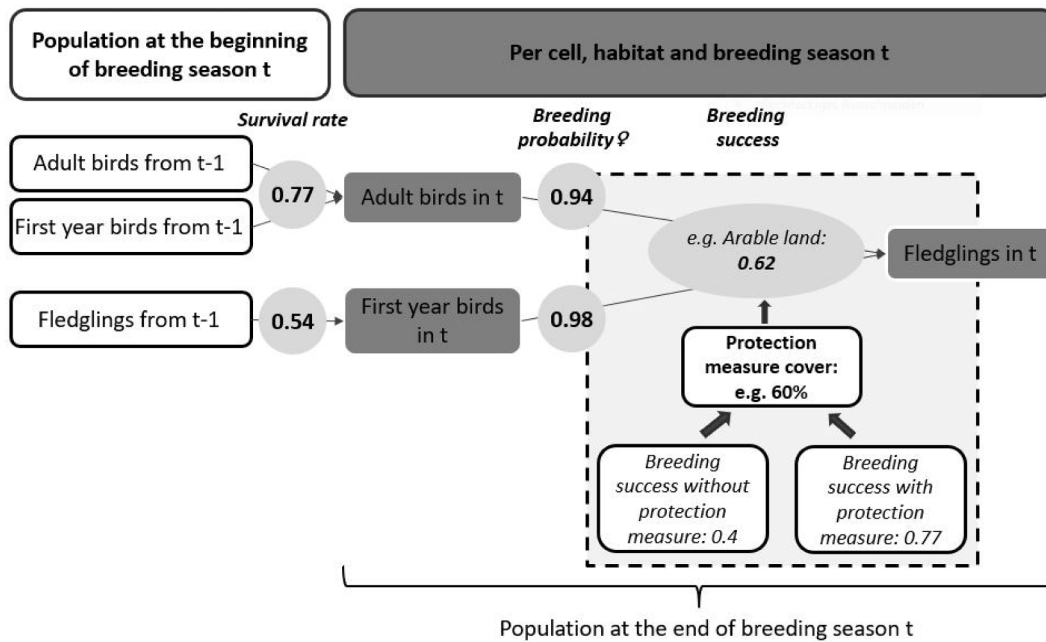


Fig. A8. Schematic representation of reproduction if conservation measures are applied. Source: own graph based on Plard et al. (2019).

#### A.3.4. Simulation of the first year

The first year in the model, as the entry into the simulation, is programmed differently from the other years. The model starts with an initial population per cell based on data from the Atlas of German Breeding Bird Species (ADEBAR) (Gedeon et al., 2014) (Section A.2.1.3). The initial population is allocated to the three habitat types in proportion to habitat availability, and all birds are considered to be adult birds. After bird allocation, a first reproduction process is simulated, analogous to Eqn 16, but without first-year birds (Fig. A9). Afterwards, year two begins with movements between cells, as described in Section A.3.1.

$$pop_{i,j,h,a=3,t} = \left( \frac{pop_{i,j,h,a=1,t} * BP_{a=1}}{2} \right) * BS_h \quad (18)$$

#### A.3.5. Calibration of the model

The aim of the model is to simulate population development so that it sufficiently corresponds to real development. To ensure this correspondence, we compared our simulation with annual population trend indices by Busch et al. (2020). Trend indices are based on the German Common Breeding Bird Survey, referring to annual observations on sampling plots randomly distributed across German regions and adequately considering different habitat types (Mitschke, Sudfeldt, Heidrich-Riske H., & Dröschmeister, 2005; Sudfeldt et al., 2012). The reported indices refer to the years 1991 to 2013 and are indexed to 2006 (value 1 = 2006). Fig. A10 depicts the indices with their standard errors,<sup>10</sup> differentiated by three German regions: northwestern (NW), southwestern (SW) and eastern (E) Germany. Regions are differentiated by the spatial structures of agricultural landscapes and geographic heterogeneity. The northwest comprises the landscape type "Atlantic lowland", whereas in the southwest, the dominant landscape type is low mountain ranges. Both represent western German landscape patterns with smaller spatial structures. The eastern region comprises larger spatial structures and continental lowland (Busch et al., 2020; Sudfeldt et al., 2012).

However, for the comparison with our simulation, we do not need a trend but rather the absolute population size (number of pairs in a given year). Therefore, we combined the trends from Busch et al. with literature data of the population from one year for each German federal state (data from Lower Saxony and Bremen are summarised) to estimate population levels.<sup>11</sup> Preferably, we used literature data from around 2006 to be as close as possible to the index year used in Busch et al. (2020). However, depending on data availability, this was not possible in all federal states. Figs. A11-A13 show the results, and the figure descriptions give the sources of the federal state population data.

After estimating the population in each federal state, we summed these populations in order to estimate the population levels per region (NW, SW, E) and for Germany in total. For validation, we compared these population levels for 2006 with region-specific population data from ADEBAR (Gedeon et al., 2014), which we processed so that they represent the initial population in the start year 2006 of our model (cf. Section A.2.1.3). The results displayed in Table A2 show that there is sufficient consistency.

However, estimated population levels refer to the development from 1991 to 2013, but the start year in our simulation is 2006 based on ADEBAR data (Gedeon et al., 2014). To generate a common starting point for the estimated populations and the simulation, we set a new initial population in the model. In each cell, we multiplied the population in 2006 (ADEBAR data) with the region-specific index values (Busch et al., 2020) to obtain the values for 1991 (NW: 2.94; SW: 2.91; E: 3.47). The generated cell-specific values for 1991 represent the starting point of the simulation, and thus, we could compare the simulated population development from 1991 to 2013 with the estimated population that is based on the index by Busch et al.

<sup>10</sup> Standard errors were kindly provided by the authors.

<sup>11</sup> In each region, the identical relative development is assumed to be equal for the respective federal states, but the number of breeding pairs is taken from the literature.



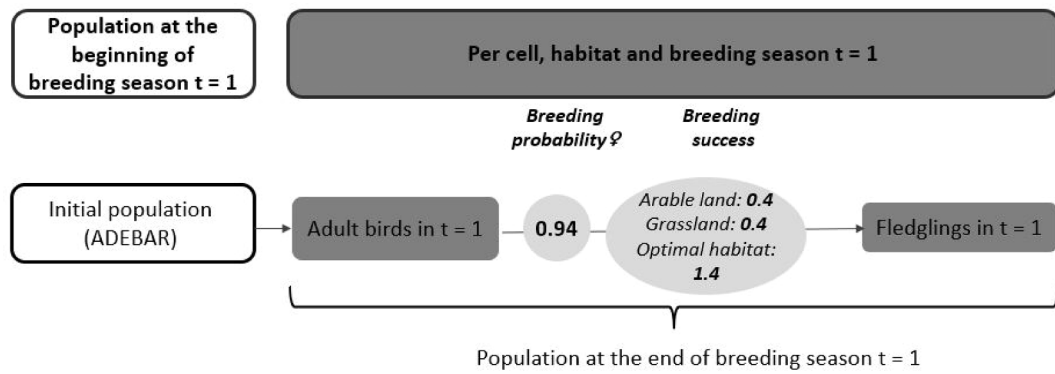


Fig. A9. Schematic representation of reproduction in season one (Source: own depiction based on Plard et al. (2019)).

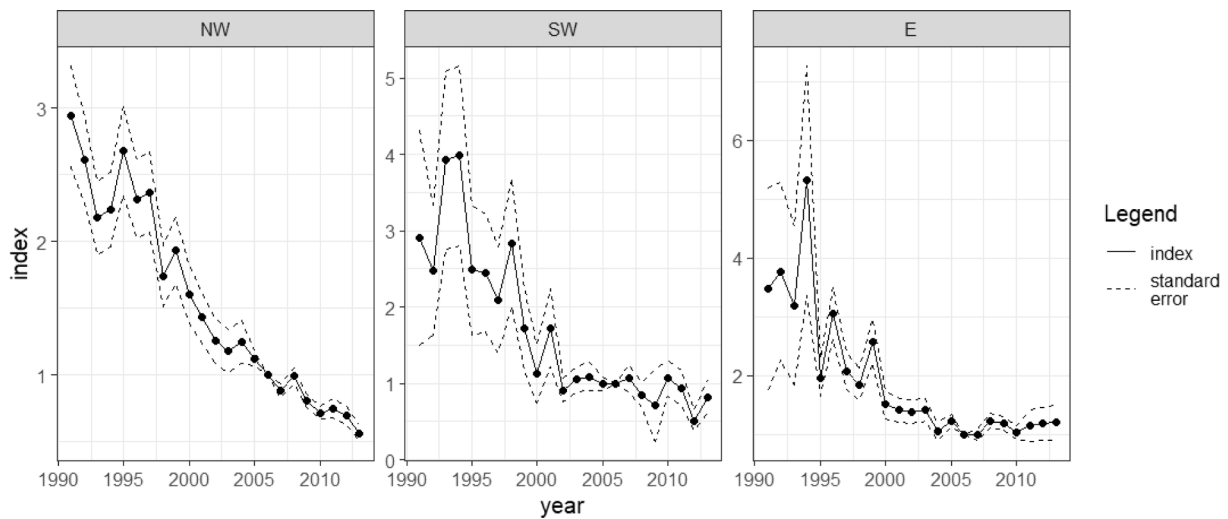


Fig. A10. Population indices and standard errors for northern lapwing from 1991 to 2013 separately for three regions of Germany: northwestern Germany (NW), southwestern Germany (SW) and eastern Germany (E). Source: Busch et al. (2020)

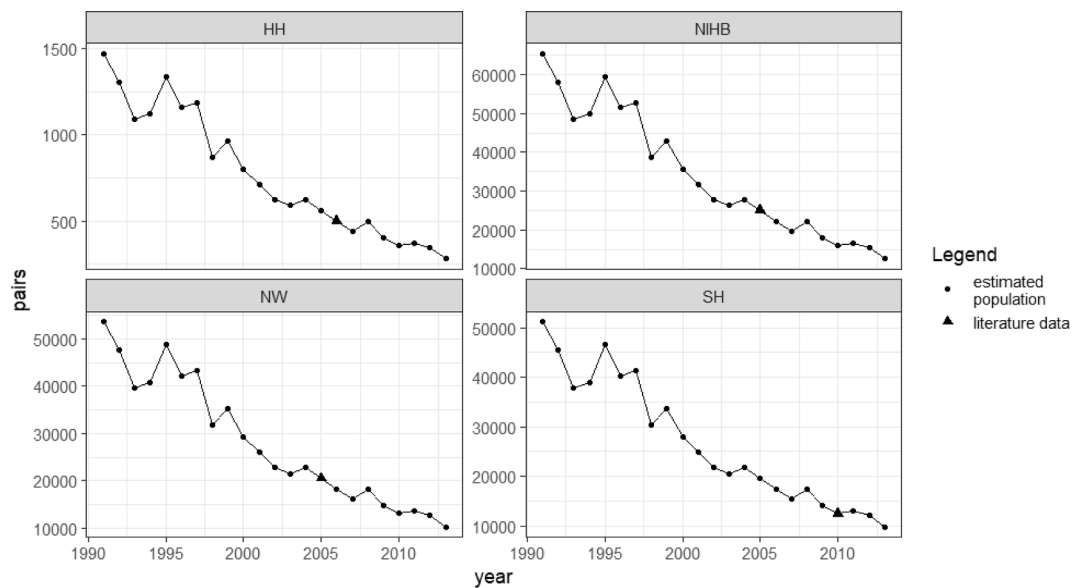
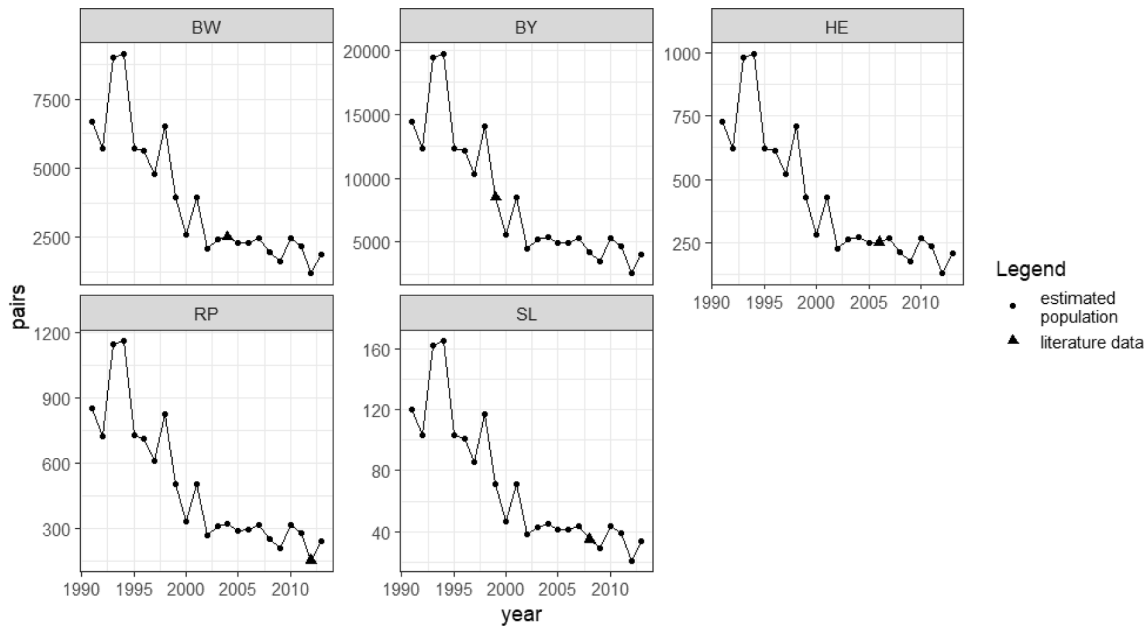
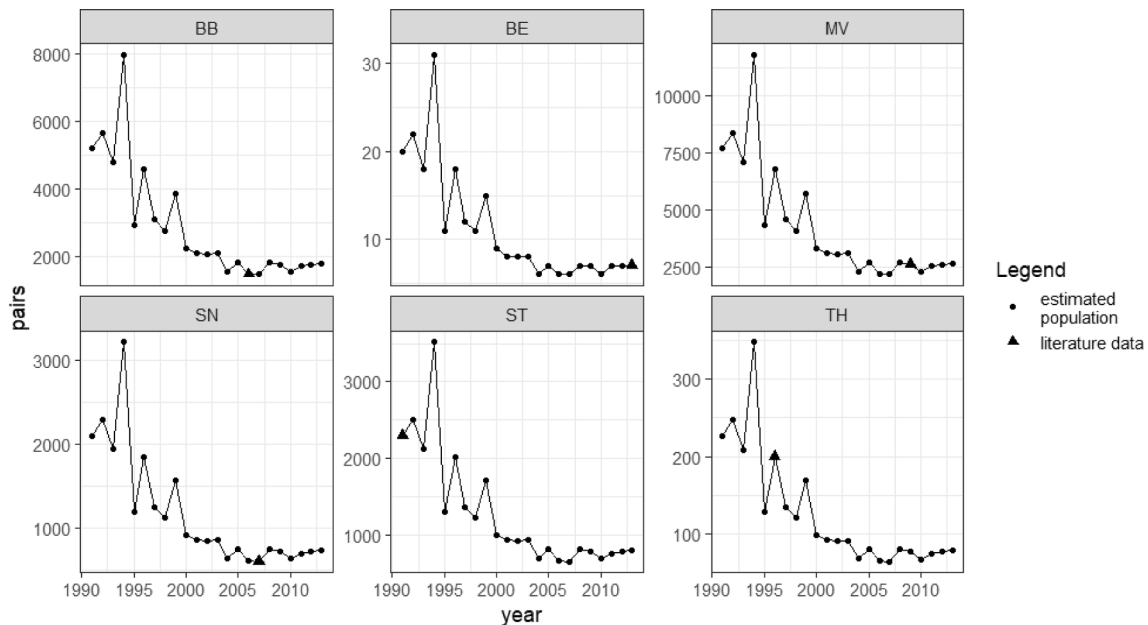


Fig. A11. Estimated population levels for northern lapwing from 1990 to 2013 for the five federal states in northwestern Germany based on the population index in Busch et al. (2020) and literature data for Hamburg (HH) in Mitschke (2006), Lower Saxony and Bremen (NIHB) in Krüger and Oltmanns (2007), North Rhine-Westphalia (NW) in Sudmann et al. (2008) and Schleswig-Holstein (SH) in Knief et al. (2010).



**Fig. A12.** Estimated population levels for northern lapwing from 1990 to 2013 for the five federal states in southwestern Germany based on the population index in Busch et al. (2020) and literature data for Baden-Württemberg (BW) in Hölzinger, Bauer, Berthold, Boschert, and Mahler (2008), Bavaria (BY) in Lossow and Fünfstück (2003), Hesse (HE) in Stübing and Werner (2017), Rhineland-Pfalz in Simon et al. (2014) and Saarland (SL) in Ministerium für Umwelt & Delattinia (2008).



**Fig. A13.** Estimated population levels for northern lapwing from 1990 to 2013 for the six federal states in eastern Germany based on the population index in Busch et al. (2020) and literature data for Brandenburg (BB) in Ryslavý and Mädlow (2008), Berlin (BE) in Witt and Steiof (2013), Mecklenburg-Western Pomerania (MV) in Ministerium für Landwirtschaft, Umwelt und Verbraucherschutz Mecklenburg-Vorpommern (2014), Saxony (SN) in Steffens, Nachtigall, Rau, Trapp, and Ulbricht (2013), Saxony-Anhalt (ST) in Schönbrodt and Schulze (2017) and Thuringia (TH) in Rost and Grimm (2004).

(2020).

For the simulation, we further compared the 1991 lapwing population (incl. chicks) per cell and habitat type with the maximum capacity (cf. Section A.2.1.2). If the 1991 population was higher, we increased the capacity to the 1991 population value. This adjustment is important to ensure that the maximum capacity is not lower than the initial population. Correction was necessary for 23 % of cells with grassland habitat, 36 % of cells with arable land habitat and 13 % of cells with optimal habitat.

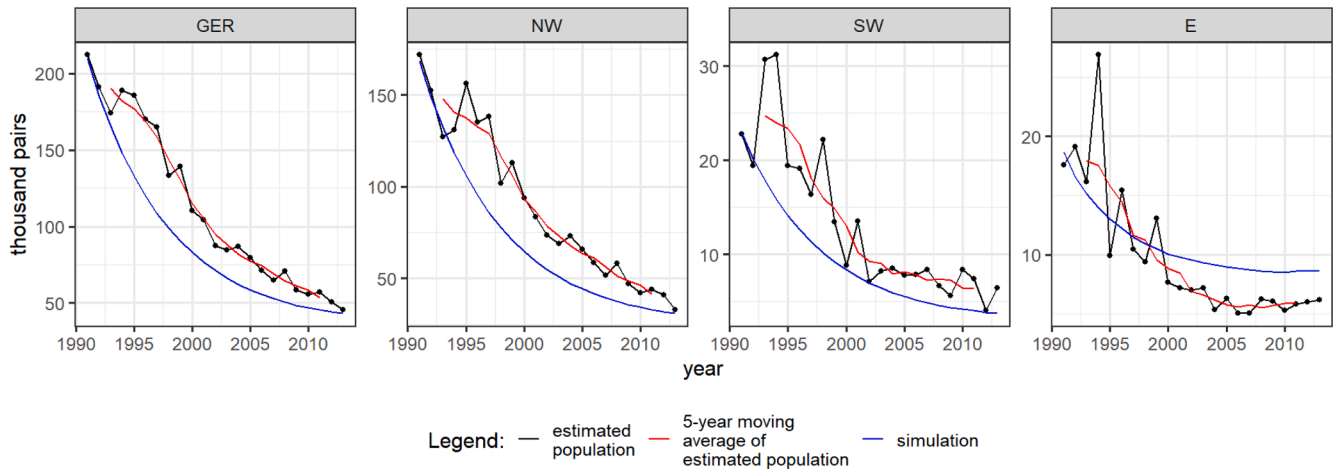
The simulation is based on input data from different sources given in Table A1. Only for own-habitat preference (OHP) no input data from the literature was available, so we used estimations. The first simulation iterations did not deliver a sufficient match with the trends. Therefore, we calibrated the model by varying own-habitat preferences within a reasonable range until we reached a sufficient match (OHP for grassland and arable land: 0.8; for optimal habitat: 0.83).

Fig. A14 shows comparisons of the estimated population and the simulation. Overall, the model is able to predict the population development over

**Table A2**

Comparison of region-specific estimated population levels (number of pairs) in 2006, based on the index by Busch et al. (2020) (column two) and data from ADEBAR (Gedeon et al., 2014), for the start year 2006 in our model (column three).

Region	Estimated population level in 2006 based on trends	ADEBAR data (start year 2006 in our model)
North-West (NW)	58 421	57 252
South-West (SW)	7 830	7 894
East (E)	5 064	5 378
Germany in total (GER)	71 315	70 524



**Fig. A14.** Population simulation in comparison to the estimated population and its five-year moving average for northern lapwing from 1990 to 2013, based on the population index in Busch et al. (2020), separately for Germany in total (GER) and three German regions (northwestern Germany (NW), southwestern Germany (SW) and eastern Germany (E)).

the 23-year period for Germany in total, and it can mimic region-specific developments, although we use global parameters in the reproduction model and for OHP (Table A1). The model cannot, however, mimic the interannual volatility.

For the total German lapwing population, we observe a very good match between the simulation and the estimated population, both showing a loss of 79 %, which is mainly a result of the match in northwestern Germany, which comprises more than three-quarters of the German lapwing population. Here, we observe a population loss of 81 % in the estimated population and 82 % in the simulation. In southwestern and eastern Germany, which comprise smaller population shares (each ~ 10 %), the differences between the estimated population and simulation are greater. For southwestern Germany, the simulated population loss is somewhat higher (84 %) than for the estimated population (72 %). In eastern Germany, the situation is the opposite; in the simulation, the population loss is only 54 % in comparison to the 65 % loss in the estimated population. However, the estimated population is subject to strong fluctuation in the first few years. Nevertheless, the model is able to depict the stabilisation phase beginning around 2005.

To conclude, with the calibrated model, we are able to reproduce region-specific lapwing population developments from 1991 to 2013 for three German regions and the total German population. Underlying parameters are thus calibrated for the period 1991 to 2013. They serve as parameters for scenarios simulating potential future developments.

### A.3.6. Scenarios and variations

**A.3.6.1. Baseline scenario in two variations.** The baseline scenario comprises a simulated population development from 2006 to 2055. This simulation shows the potential population development in the three habitat types if land use is stable and no conservation measures are taken. Furthermore, within the baseline scenario, we differentiated between a best-case and worst-case variation to account for uncertainty in our data on optimal habitat availability. We consider the best-case variation to be at the upper end of a possible range of developments. In the best-case variation, all values were included as described in the previous sections. However, the availability of optimal habitat in our model may be overestimated because, for example, in the identified optimal habitat areas, conditions for the lapwing might not be as optimal as assumed everywhere (cf. Section A.2.1.1). Thus, the optimal habitat population could be overestimated in the best-case variation, and we additionally set up a worst-case variation, which we consider to be the lower end of a range of possible developments without conservation measures. In this variation, we limited the capacity in the optimal habitat to the best-case simulated optimal habitat population of 2021.

**A.3.6.2. Conservation measure scenarios including cost calculation.** In five conservation measure scenarios, we simulated cases in which different population shares between 20 % and 100 % are protected by measures from 2021 onwards for both arable land and grassland. Thus, we assumed that in arable land, lapwing plots are implemented and that a similarly effective measure is implemented in grassland. Conservation measure scenarios include best-case and worst-case variations under the same conditions as in the baseline scenario.

The cost calculation refers only to lapwing plots inhabiting arable land. Costs are initially calculated for arable land in each cell and year. First, the number of protected pairs is determined. In each cell, the number of birds (adult + first-year birds) is divided by two to form pairs and then multiplied by the share of protected pairs, as costs incur only for these pairs.

$$\text{number of protected pairs}_{i,j,t} = \frac{\text{POP}_{i,j,t} * \text{share of protected pairs}}{2} \quad (19)$$

Then, the required number of hectares of lapwing plot are determined by multiplying the number of protected pairs by 0.4 ha, which is the average requirement per pair.

$$\text{required hectares}_{i,j,t} = \text{number of protected pairs}_{i,j,t} * 0.4 \text{ ha} \quad (20)$$

Finally, the required number of hectares per cell is multiplied by the cell-specific weighted average gross margin (WAGM), and the results are summed over all cells, resulting in total costs per year.

$$\text{total costs}_t = \sum_{i,j} (\text{required hectares}_{i,j,t} * \text{WAGM}_{i,j}) \quad (21)$$

## Appendix B. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jnc.2022.126314>.

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