



K O N I N K L I J K E N E D E R L A N D S E
A K A D E M I E V A N W E T E N S C H A P P E N

Low productivity and unsuitable management drive the decline of central European lapwing populations

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published in

Animal Conservation
2020

DOI (link to publisher)

[10.1111/acv.12540](https://doi.org/10.1111/acv.12540)

document version

Peer reviewed version

[Link to publication in KNAW Research Portal](#)

citation for published version (APA)

Plard, F., Bruns, H. A., Cimiotti, D. V., Helmecke, A., Hötker, H., Jeromin, H., Roodbergen, M., Schekkerman, H., Teunissen, W., van der Jeugd, H., & Schaub, M. (2020). Low productivity and unsuitable management drive the decline of central European lapwing populations. *Animal Conservation*, 23(3), 286-296.
<https://doi.org/10.1111/acv.12540>

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Low productivity and unsuitable management drive the decline of central European lapwing populations

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Abstract

Despite the protective measures that have been implemented to increase the productivity
3 of meadow birds, populations are still declining in most breeding and wintering areas.
We therefore still do not know how large the protective efforts need to be to curb the
decline of the meadow bird populations. By taking advantage of monitoring data from
6 the populations of lapwings in the Netherlands (NL) and one region in Germany (SH),
we investigated the demographic drivers responsible for the decline of the populations
and evaluated the impact of protective measures. In these populations, some nests are
9 marked with sticks such that they are not destroyed by farming activity. We analyzed
the data with integrated population models and show that average demographic rates
were similar in the two populations. Retrospective analyses demonstrated that variation
12 in productivity most strongly impacted population dynamics and that its variation was
influenced by the local environments. Our results confirmed that low productivity (0.55
and 0.46 fledglings per pairs in SH and NL, respectively) was the main reason for the
15 decline of the lapwing populations. Productivity of 0.76 (SH) and 0.91 (NL) fledglings
per pairs would be required to stabilize the populations. The implemented nest pro-
tection had a positive effect on nest success, but did not improve chick survival, and
18 consequently the effect on population growth rates remained insufficient. The popu-
lation growth rate in NL would increase by only 2% if all nests were protected. Our
results suggest that protective measures should prioritize the reduction of predation and
21 the improvement of chick habitat by promoting heterogeneous swards combining tall
vegetation for hiding and short and open vegetation for foraging.

Keywords: management scenarios, meadow birds, population viability analyses, prospec-
24 tive analysis, retrospective analysis, sustainable reproductive success

1 Introduction

Species conservation requires a good understanding of the demographic drivers underpinning population change (Martin *et al.*, 2007; Wilcove & Wikelski, 2008). However, the spatial distribution of declining species may preclude the application of general conservation or management plans, because different populations of the same species are often managed by different institutions and thus through different measures. To assess the decline of species and set up more widely efficient management plans, information about different populations must be gathered. Models of population dynamics that focus on one site only may neither be representative of the dynamics at other sites, nor of the global dynamics. Comparing the dynamics of different breeding populations offers also the advantage to distinguish between global and local dynamics (Frederiksen, Harris & Wanless, 2005; Schaub, von Hirschheydt & Gruebler, 2015).

Many populations of waders are strongly declining in Europe, in particular species whose originally breeding habitat were wet meadows (Chamberlain *et al.*, 2000; Donald, Green & Heath, 2001; Roodbergen, van der Werf & Hötker, 2012). The demography of these wader species is poorly studied at large spatial scales, but declines at smaller spatial scales were mostly attributed to declines in productivity (Besbeas *et al.*, 2002; Roodbergen, van der Werf & Hötker, 2012) caused by the loss and intensification of agricultural management or an increase in predation. Agricultural landscapes have become homogeneous (Benton, Vickery & Wilson, 2003; Donald, Green & Heath, 2001), and the loss of wet habitats has reduced the availability of resources for waders. Moreover, predators may have increased, and may be able to locate clutches and hatchlings while still flightless more easily in homogeneous landscapes (Schekkerman, Teunissen & Oosterfeld, 2009). An illustration of such a major decline is the decrease of Northern lapwing

(*Vanellus vanellus*, referred to as lapwing) populations. This species used to be a common agricultural bird in Europe up to the 1980s, but has obtained the status Near-Threatened
51 since 2015 (BirdLife International, 2017).

The lapwing is a medium-sized wader which is migratory over most of its range (Shrubb, 2009). Lapwing females generally lay 4 eggs in variable habitats such as wet-
54 lands and grasslands but also on arable lands. They can lay replacement clutches if clutches fail. After an incubation of 24-28 days, hatchlings leave the nest and are guided by the parents until they fledge. The western European population of lapwing is migra-
57 tory and spends the non-breeding season mainly in Southwestern Europe and Northern Africa. Lapwings are hunted along their migratory routes or in their wintering areas (Petersen, Trollet & The European Commission, 2009). However, a recent study suggested
60 that hunting was not the main driver of population decline (Souchay & Schaub, 2016). Most evidence indicates that the decline of the lapwing was linked to a decrease in productivity, as is the case in other wader species (Shrubb, 2009). Lapwing nests are
63 vulnerable to predation because they are placed on the ground. Successful lapwing productivity requires both dry areas for placing the nest and nearby wet areas for foraging (Chamberlain & Crick, 2003; Eglinton *et al.*, 2010). After hatching, survival of the
66 self-feeding precocial chicks depends on suitable habitat with patches of vegetation to hide themselves and patches of bare ground allowing easy access to food (Johansson & Blomqvist, 1996). Chicks are particularly vulnerable during this period, and many of
69 them are predated (Mason, Smart & Drewitt, 2018; Schekkerman, Teunissen & Oosterveld, 2009). The intensification of agricultural practices has degraded chick habitat with a decline in invertebrate biomass in cultivated fields, reducing the availability of acces-
72 sible food for chicks (Devereux *et al.*, 2004; Kentie *et al.*, 2013; Schekkerman & Beintema,

2007).

Some lapwing populations are managed with the aim of increasing productivity. While productivity of some waders has increased, their decline has not been reversed (Breeuwer *et al.*, 2009; Franks *et al.*, 2018; Walker *et al.*, 2018). The efficiency of management measures such as land management have been evaluated using correlation between abundance and productivity and do not account for the demography of the global European population (Franks *et al.*, 2018; Żmihorski, Kotowska & Pärt, 2016). Some management measures aim for direct protection of lapwing nests. These applied measures differ and range from marking the nests with sticks such that they are not destroyed by farming activity to fencing single nests or breeding colonies with the aim to exclude ground predators (Rickenbach *et al.*, 2011). However, nest protection does not impact food availability and most types of nest protection do not protect chicks from predators after hatching. The impact of the protective measures in breeding sites on population dynamics still needs to be evaluated. All these measures are costly as they imply human time and farmer remuneration to implement management or protective measures (for instance, in North Germany, 350€ per hectare meadow are given to the farmers to delay mowing where lapwings are nesting). As a consequence, a robust analysis determining if the protective measures allow reaching the required reproductive success to achieve a stable population is still needed to assess if these measures are sufficient for halting the population decline at large spatial scales.

In this study, we built two independent integrated population models (IPM, Besbeas *et al.* 2002; Schaub & Abadi 2011) to compare demography and drivers of two breeding populations in the Netherlands and in Northern Germany. The Netherlands population includes the complete national population while the data from Northern Germany origi-

nate from three main sites. We took advantage of these two long-term datasets that differ in spatial and temporal scales and type of data collected, to evaluate the drivers of the decline of these lapwing populations. We performed population viability analyses for each breeding population, including uncertainty in demographic rates (Oppel *et al.*, 2014; Saunders, Cuthbert & Zipkin, 2018). Finally, we investigated the efficiency of protective measures on productivity and population dynamics.

2 Methods

Studied populations and data

We used data from two populations: the population in the Netherlands (NL), and a population in the German federal state Schleswig-Holstein (SH). For both populations, we jointly analysed population counts, data about reproductive success, and capture-recapture-recovery data. The type of data differed between the two populations due to different field protocols.

For NL, we used recaptures and dead recoveries of birds ringed in the Netherlands from 1995 to 2015. Birds could be ringed as chicks, juveniles (fledglings) or as adults (N= 25,079 chicks, 675 juveniles and 2,236 adults). Birds were sexed if they were (re)captured or (re-)observed when at least one year old (e.g. ringed in June as a chick and resighted in March of the following year as a male or female), but some remained unsexed. The capture histories of unsexed birds were used to estimate survival, but not breeding probability. Breeding status was known for birds captured on or close to their nests. The Dutch lapwing nest record scheme monitored 213,797 nests from 1995 to 2014 in different places across the Netherlands (on average, 10,960 nests/year, from 38 nests in

1995 to 19,064 nests in 2006). The breeding success from monitored nests was used to
120 estimate productivity. The nests are spread over the country and over habitats such that
these data inform us about global nest success in the NL. Most (99%) monitored nests
were marked with sticks to avoid destruction by agricultural activities and to ensure
123 recovery of nests to monitor nest success. For each nest, the clutch size, the number of
days the nest was monitored, the breeding success (successful: hatching of one egg at
least /not successful), and the protection status (protected using sticks/not protected)
126 were recorded. This status was used to estimate the influence of nest protection on nest
survival, productivity and population growth rate. The number of hatched or fledged
chicks per nest was not recorded. The national lapwing breeding index (van Turnhout
129 *et al.*, 2008) was used for a measure of population size.

In SH, the population has been monitored from 2007 to 2016 in 3 main sites (1,715 ha
in total): Tollenmoor, Meggerkoog and Dithmarscher Eidervorland. The first two sites
132 are located in the Eider-Treene-Sorge region, a wet floodplain dominated by grassland.
The latter site is a marsh in the estuary of river Eider. Birds were ringed and colour
marked near fledgling or as adults (N= 317 juveniles and 170 adults) between March and
135 July each year, and re-observed in successive breeding seasons. Information about the
breeding status of marked birds was also collected. Birds that were observed displaying
territoriality, courtships, or nesting including chick-rearing behavior were considered as
138 breeding individuals. Other birds had an unknown breeding status. To assess annual
productivity, data on the annual number of fledglings was collected from 108 to 202
pairs annually. Chicks were monitored every five days for at least 21 days after hatching
141 before counted as fledged. The number of chicks per successful pair could sometimes
be underestimated because chicks were hidden in high vegetation. Almost all nests

were marked in this monitored population with sticks and farmers delayed agricultural
 144 activities that might destruct lapwing nests. Finally, the sum of observed breeding pairs
 in the study sites was used as an index of population size.

2.1 Integrated population models

147 We developed an integrated population model (IPM) for each population to analyse
 jointly the different data sets (capture-recapture-recovery data, reproductive data, and
 population index data). The two IPMs were based on a female pre-breeding population
 150 with two age classes (first-year and adult). In the following we describe the likelihoods
 of each data set. For the population index data a state-space model was developed. The
 state processes are described by the following matrix projection models:

For NL:

$$\begin{bmatrix} N_{t+1}^j \\ N_{t+1}^a \end{bmatrix} = \begin{pmatrix} \Psi^j \frac{P_t}{2} S_t^j & \Psi^a \frac{P_t}{2} S_t^j \\ S_t^a & S_t^a \end{pmatrix} \begin{bmatrix} N_t^j \\ N_t^a \end{bmatrix}$$

For SH:

$$\begin{bmatrix} N_{t+1}^j \\ N_{t+1}^a \end{bmatrix} = \begin{pmatrix} \Psi^j \frac{P_t}{2} S_t^j & \Psi^a \frac{P_t}{2} S_t^j \\ S_t^a & S_t^a \end{pmatrix} \begin{bmatrix} N_t^j \\ N_t^a \end{bmatrix} + \begin{bmatrix} 0 \\ I_t \end{bmatrix}$$

153 Where N_t^j and N_t^a are the indices of first-year and adult individuals and S_t^j and S_t^a
 are the annual first-year and adult survival. P_t is the annual productivity defined as the
 annual number of fledglings produced per female. Ψ^j and Ψ^a are the breeding proba-
 156 bility of first-year and adult birds, but they are defined differently in the two breeding
 populations due to different methods of data collection (see above). Breeding proba-
 bility is defined as the probability of an individual to nest and as the probability that
 159 an individual has a territory in NL and SH, respectively. Because the data on breeding

status were sparse in both breeding populations, breeding probabilities were kept constant across years. The NL population was assumed to be geographically closed because
162 of its large spatial extension. Moreover, true survival was estimated by the inclusion of recovered dead individuals. By contrast, the SH population was assumed to be geographically open due to its small spatial extend and thus to be subject to emigration
165 and immigration. Since no dead recoveries of marked individuals were available, the estimated survival is apparent and thus emigration is already accounted for, although not estimated explicitly. The joint analysis of the different datasets allowed the estimation of
168 immigration in this population (I_t is the number of immigrants) (Abadi *et al.*, 2010).

For both populations we used a Poisson distribution to link the predicted population index with the population index data.

171 **Productivity**

As we did not have direct information about the number of fledglings produced per female in NL, we calculated the productivity from: $P_t = E_t * H_t * S_t^c + (1 - H_t) * R * E_t * H_t * S_t^c$ where E_t is the annual clutch size, H_t is the hatching probability in year t , S_t^c is the chick survival (the probability for a bird marked as chick to survive until fledging), and R is the probability for a female to lay a replacement clutch. The first part of this
174 sum models the number of fledglings produced when a female had a successful first
177 clutch, and the second part of this equation models the number of fledglings produced by a replacement clutch. We neglect the possibility that females may lay more than one
180 replacement clutch. Chick survival was estimated using the multi-event model described in detail in Appendix S1. Clutch size was estimated using data on clutch sizes in the monitored nests. The hatching probability was estimated using the daily survival of
183 monitored nests with the Mayfield method (Mayfield, 1975). We tested the influence

of protection status on hatching probability. The probability for a female to produce a replacement clutch was estimated without explicit data in the IPM and kept constant
186 across years.

Productivity was directly assessed using the annual mean number of fledglings per territory (P_t) in SH. We used a normal distribution to model this variable and added the
189 site (Tollenmoor, Meggerkoog and Dithmarscher Eidervorland) as a random effect to take into account variation in habitats between the three sites. As all nests were protected, estimated productivity already included the influence of nest protection in SH.

192 **Multi-event model to estimate survival and breeding probabilities**

We used a multi-event model to jointly estimate survival and breeding probabilities. The models used for each population as well as the goodness of fit tests are detailed in
195 the Appendix S1.

A pre-analysis using a Cormack-Jolly-Seber model found no difference between male and female survival (sex effect: mean: -0.05 and 95% credible interval: [-0.81;0.86] in SH),
198 and consequently annual survival was modeled with an age-effect, only. The breeding probability has been reported to vary with age and sex in lapwings (Lislevand, Byrkjedal & Gronstol, 2009; Parish, Thompson & Coulson, 2001; Thompson *et al.*, 1994), and
201 therefore we kept it sex and age-dependent in our models. The probability of correctly recording the breeding status was kept sex-dependent, as female breeding status was often easier to determine because they spent more time incubating eggs than males.
204 However, a difference in the ability to determine breeding status was not expected for different ages. Because first-year individuals tend to migrate further and may suffer different sources of mortality than adults, recovery probabilities included an age effect, but
207 no sex effect. Recapture probabilities included an age effect (first-year vs. after first year

recapture) in both population models, a trap effect in the SH model (trap-happiness due to the increased re-sighting rate of birds with known territories) and a sex effect in the
210 NL model (females were easier to capture when they were on the nest than males).

We used the Bayesian framework to build the two IPMs using JAGS (Plummer, 2003) through the package jagsUI (Kellner, 2015) in R (R Core Team, 2014). We specified vague
213 priors using normal distributions of mean 0 and variance 1,000 for most parameters. Uniform distributions over the interval [0;10] were used as priors for standard deviation of the random effects. Because of the low number of years for the SH population, we
216 used informative priors based on previous studies on lapwing breeding probability. We specified uniform distributions over the interval [0.6;1] and [0.1;0.9] for adult and first-year breeding probabilities, respectively (Lislevand, Byrkjedal & Gronstol, 2009; Parish,
219 Thompson & Coulson, 2001; Thompson *et al.*, 1994). We have performed a prior sensitivity analysis for these parameters by comparing results when different priors have been used. Our results showed that the posterior distributions of breeding probabilities
222 were little sensitive to the specific priors (Table S2, Fig. S1). We ran 3 chains with 75,000 iterations, discarded the first 30,000 as burn-in, and checked convergence of all parameters with the Rubin and Gelman convergence diagnostic (Gelman & Rubin, 1992). We
225 generally report posterior means and the limits of the 95% credible intervals (CRI) of the estimated parameters.

2.2 Prospective and Retrospective analysis

228 We performed prospective analyses and estimated the elasticities of the population growth rates to each demographic rate by prospective simulations. Elasticities inform us about how much the population growth rate would change if each demographic rate changed

231 by 1% in turn. Second, we performed retrospective analyses to determine the demo-
graphic drivers of both populations. Specifically, we estimated the contribution of the
temporal variation in each demographic rate to the variation in the realized population
234 growth rates (Koons, Arnold & Schaub, 2017).

2.3 Population viability analysis

First, we performed a population viability analysis (PVA) for each breeding population.
237 We assumed that demographic rates were stationary (same means and temporal vari-
abilities of the demographic rates in the future as during the study periods (Table S1))
and predicted the population dynamics for the next 15 years (until 2030).

240 Second, we calculated how much (in %) each demographic rate needs to increase in
order to reach stable populations (i.e. $\lambda = 1$).

Third, because environmental fluctuations may cause the efficiency of management
243 measures to be variable, we estimated how often a high productivity year should occur
for the breeding populations to remain stable. The temporal variance in productivity
(Table S1) was used to simulate 1000 years with variable productivity. A high produc-
246 tivity year was defined as a year belonging to the 5% best years in terms of productivity
in each population. We simulated populations where these high quality years occurred
more and more frequently (from 10% to 100% of the years) and estimated the corre-
249 sponding stochastic population growth rates, defined as the mean of the logarithm of
realized population growth rates over the next 100 years.

3 Results

252 3.1 Population dynamics and demographic rates

Indexes of population size have declined in both populations during the study period (by 32% and 34% in 10 years in SH (2007-2017) and NL (2005-2015), respectively, and 255 53% in 21 years in NL over the study period, Fig. 1A-B). Annual population growth rate of both populations was below 1 in most years (Fig. 1I-J), but had no negative trends (slopes: <0.001 , CRI:[-0.003;0.003] and 0.02 [-0.001;0.042] in NL and SH, respectively) 258 showing that the speed of the decline did not accelerate.

Estimates of average demographic rates were slightly higher in SH than in NL (Table 1). First-year survival was estimated at 0.62 [0.48;0.78] and 0.57 [0.40;0.78], and adult 261 survival was 0.81 [0.74;0.88] and 0.77 [0.73;0.81], on average for SH and NL, respectively (Fig. 1E-F). Estimated immigration into the SH population was very low (Fig. 1C).

Mean productivity (the number of fledglings per female) was low in both populations 264 (0.46 [0.26;0.72] and 0.55 [0.27;0.87] for NL (for unprotected nests) and SH, respectively). Temporal variation in productivity was not synchronous in the two populations (Fig. 1G-H), with relatively high productivity in springs 2010 and 2014 in SH vs. springs 2011 and 2012 in NL. Productivity in the NL population was calculated based on the estimates of hatching probability and chick survival. The hatching probability was 0.44 [0.39;0.49], on average, and the chick survival was 0.18 [0.13;0.25], on average, and was more temporally 267 variable than the hatching probability (Fig. 1). The probability of laying a replacement clutch was estimated at 0.95 [0.82;1.00]. The breeding probability of females was similar in yearling and adult females (0.98 [0.93;1.00] and 0.94 [0.85;1.00] in NL, respectively). 270 These rates were lower in SH (0.70 [0.49;0.88] and 0.84 [0.70;0.99] for yearling and adult 273

female breeding probabilities, respectively).

The protection of nests improved daily nest survival (slope: 0.40 [0.30;0.50]). As a
276 result, productivity in NL increased from 0.46 when nests were not protected to 0.54
when nest were protected. This last value is similar as the productivity in SH (0.55, Table
1) where all monitored nests are protected. Population growth rate increased from 0.88
279 to 0.90 if no vs. all nests are protected in NL. Thus, the kind of nest protection used in
SH and NL is not sufficient to allow the recovery of the Dutch or the German lapwing
populations even if it would be applied on all nests.

282 **Prospective and Retrospective analyses**

The elasticity analyses showed that adult survival was the demographic rate with the
highest potential impact on the dynamics in both populations (Fig. 2A-B). Yearling sur-
285 vival, productivity and adult breeding probability had similar, but lower potential im-
pact on the population dynamics, and yearling breeding probability and the population
structure had almost no potential impact.

288 The retrospective analyses revealed that variation in productivity was, by far, the
main driver of the actual variation of the growth rates of both populations (Fig. 2C-D).
The variation of adult survival also contributed relatively strongly to the dynamics of the
291 NL population, mainly because of the low adult survival probability in 2006/2007.

Population viability analyses

The predictions of the PVAs showed that both populations would continue to decline
294 if the means and temporal variabilities of the demographic rates remain the same as
observed in the past. The NL population would decrease below the threshold of 5% of

the population index in the first year of the study in 2030 with 50% chance (Fig. 3). The
297 high uncertainty of the predictions in SH prevents reasonable conclusions about possible
extinction.

The two populations would become stable ($\lambda = 1$) if either the productivity would
300 reach 0.76 and 0.91 fledglings per pair in SH and NL, respectively, or if the adult survival
would increase by 6% in SH and 16% in NL (to 0.86 and 0.89). An increase of first year
survival to 1 would not allow the populations to stabilize.

303 If high productivity is achieved in three over four years (73% of years with pro-
ductivity higher than 0.78 fledglings per pair) the SH population would become stable
($\lambda_s = 1$). For the NL population, the frequency of high productivity years (higher than
306 0.82 fledglings per year) would have to increase to 0.91 to achieve a stable population.

4 Discussion

The two studied lapwing populations had very similar average demographic rates and
309 were subject to the same demographic drivers. Although the SH study site was smaller
than the NL study site, low immigration and similar adult survival rates suggested that
immigration and emigration had weak influence on population dynamics. The retrospec-
312 tive analyses showed that variation in the annual productivity had the largest impact on
the population growth rates in both populations, suggesting that low productivity was
the main demographic reason for the decline of central European lapwing populations.
315 These results are in agreement with previous studies that have evidenced low hatching
and fledgling success to be the main demographic drivers for lapwing population de-
clines (Besbeas *et al.*, 2002; Chamberlain & Crick, 2003; Mason, Smart & Drewitt, 2018;
318 Peach, Thompson & Coulson, 1994; Schifferli, Spaar & Koller, 2006) and for other grass-

land wader species (Roodbergen, van der Werf & Hötker, 2012).

Despite the large potential impact of adult survival on lapwing population dynamics,
321 it contributed little to the past dynamics, because it showed little temporal variability.
Our estimates of adult survival were comparable with previous demographic studies
(Besbeas *et al.*, 2002; Peach, Thompson & Coulson, 1994; Souchay & Schaub, 2016), show-
324 ing that in most of its range, annual survival remained stable since the sixties (Peach,
Thompson & Coulson, 1994). Despite hunting and the high elasticity of the population
growth rate to adult survival, our results are in accordance with the analysis of Souchay
327 & Schaub (2016) and suggest that observed variation in the population growth rate was
not mainly influenced by variation in survival. Lapwing population dynamics is thus
mainly driven by the temporal variation in productivity as in many other bird popula-
330 tions (Saether *et al.*, 2016). Immigration had a weak impact on the population dynamics
of the SH population, which may be due to the high philopatry of lapwings (Lislevand,
Byrkjedal & Gronstol, 2009). Due to the slightly higher survival rates in SH, the gap
333 between observed and needed reproductive success for the population to remain stable
is smaller in SH (0.55 to 0.76 fledglings per pair) than in NL (0.54 to 0.91 fledglings
per pair). Taking account of environmental stochasticity, years of very high productivity
336 (above 0.8) should occur in 73% and 90% of the years for the SH and NL populations to
remain stable.

Our analyses showed that a lapwing population needs a productivity > 0.8 fledglings
339 per female to be stable. This target is challenging to achieve through management ac-
tions. Even if almost all nests are marked to prevent nest failure due to agricultural
practices, it is not enough for the populations to stabilize. Nest protection increased
342 the population growth rate by only 2% in NL. Even if these protective measures are not

sufficient, it does not mean that they are not needed. Indeed, destruction of wader nests by agricultural activities has been demonstrated as a main driver of nest failure (Shrubb, 2009). However, a main problem with these applied protective practices is that they do not prevent predation and do not improve habitat quality. When ground predators are excluded by the installation of fences around large areas (a field) productivity can be significantly increased. Productivity increased from 0.23 to 0.79 fledglings per pair in England (Malpas *et al.*, 2013) and chick survival increased from almost 0% to 24% in Switzerland (Rickenbach *et al.*, 2011) after the construction of fences around fields. The main drawback of fencing at large scales is that it is hardly possible to be applied widely due to high costs.

The different temporal patterns of productivity in the two populations suggested that productivity was influenced by local rather than by global environmental factors. Large-scale weather effects like NAO are therefore unlikely drivers of the variability in productivity. Predation is known to be the main cause for nest failure and chick mortality in lapwings and other wader species (Baines, 1990; Schekkerman, Teunissen & Oosterveld, 2009; Seymour *et al.*, 2003). Thus, the site-specific variation in annual productivity might be linked to annual variation in predator density (Mason, Smart & Drewitt, 2018). Productivity would therefore be enhanced by a reduction of predation rate. Predator density is particularly difficult to control (Bolton *et al.*, 2007) and often influences the abundance of other predators. Consequently, the effect of predator control on predation rate is rarely predictable. Other management measures involving predator exclusion using fences or cages around nests have also some inconvenients. While they are efficient in increasing chick survival, they are costly and timely to maintain (Smith *et al.*, 2011). Moreover, other predators such as corvids or raptors may learn to recognize fenced ar-

369 eas to locate nests or chicks (Koenen, Utych & Leslie, 1996; Murphy *et al.*, 2003). In the
same way, sticks could be used by terrestrial and aerial predators to find nests and can
372 increase predation rates. Lapwing are colonial breeders and defend themselves against
predators when breeding in colony by early detection of predators (Galbraith, 1988). In-
deed predation rate have been show to decrease with nest densities in many lapwing
372 populations (MacDonald & Bolton, 2008; Sálek & Smilauer, 2002; Seymour *et al.*, 2003).
Even the hatching success of other wader birds can be favoured by breeding close to
lapwing colonies (Elliot, 1985). Therefore, landscape management that operate at large
375 surfaces but result in a small-scaled combination of flooded patches, bare ground and
patches with dense vegetation should be implemented to enhance large lapwing breed-
ing colonies. Indeed, habitat quality has been reported as a crucial component for chick
378 survival in waders. While dense vegetation allows the chicks to hide from predators,
sparsely vegetated patches favour their foraging abilities (Devereux *et al.*, 2004). For
instance, body mass of Black-tailed Godwit (*Limosa limosa*) chicks that grew up in in-
381 tensively farmed grassland (monocultures) was significantly lower than body mass of
conspecifics from more natural grasslands (Kentie *et al.*, 2013), suggesting that food sup-
ply, accessibility or quality is reduced in monocultures compared to natural grasslands
384 (Schekkerman & Beintema, 2007).

5 Conclusion

Our study provides strong evidence that low productivity is the main driver of the de-
387 cline of the central European lapwing population. Even if nest protection positively
influenced productivity, it was not sufficient for the population to recover. We need
more effective predation management. Because predator controls are rarely effective,

390 agri-environment schemes (AES) as land management and agricultural practices appear
to have high potential impact on productivity of lapwing and likely other wader species
living in similar habitats (Breeuwer *et al.*, 2009; Roodbergen & Teunissen, 2014). In arable
393 land, 'lapwing plots' (fallow plots within a field, see Schmidt *et al.* 2017; Sheldon, Chaney
& Tyler 2007) could enhance breeding conditions for lapwings. The implementation of
effective AES will be essential for enhancing the reproductive success of lapwings and
396 therefore for a population recovery. Applied research and monitoring of AES is impor-
tant to ensure sustainable reproductive success (Galbraith, 1988; Kleijn & Sutherland,
2003).

399 **Authors' contributions.** MS and FP designed the study. FP carried out the analysis
and wrote the manuscript. MS, DC, MR, WT, HS, HH and HvJ provided substantial
comments to the manuscript. HB, DC, AH, HH, HJ, MR, HS, WT and HvJ provided the
402 data. All authors gave final approval for publication.

Acknowledgements

We are grateful to Natalie Meyer, Jan Sohler and the many volunteers that have collected
405 the data and to Reto Spaar, Petra Horch, Guillaume Souchay and an anonymous reviewer
for helpful discussion about the manuscript. We thank LandschappenNL and Aad van
Paassen for providing a large part of the data on nest success. The study in Schleswig-
408 Holstein was supported by the German Federal Agency for Nature Conservation (BfN)
with resources of the Federal Program for biological diversity (Bundesprogramm Biol-
ogische Vielfalt) from the German Federal Ministry for the Environment, Nature Con-
411 servation and Nuclear Safety as well as funds of the Ministry of Energy, Agriculture,
Environment, Nature and Digitalization of Schleswig-Holstein and the Hanns R. Neu-

mann Foundation (period 2014 to 2018). Previously, the study was financed by the state
414 government of Schleswig-Holstein (period 2007 to 2013).

Data accessibility. Data would be made available after acceptance of the paper.

Competing interests. We declare we have no competing interests.

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Table 1: Posterior means with their 95% credible intervals of the average demographic rates of lapwings obtained from 2007 to 2016 in Schleswig-Holstein, and from 1995 to 2015 in the Netherlands. The probabilities of recapture of adult birds that have been captured or not in the previous year in the population of Schleswig-Holstein are noted with R and NR, respectively.

	Schleswig-Holstein			The Netherlands		
	<i>mean</i>	2.5%	97.5%	<i>mean</i>	2.5%	97.5%
Survival						
First-year	0.63	0.49	0.79	0.54	0.38	0.73
Adult	0.81	0.74	0.88	0.77	0.73	0.81
Recapture probability	<i>mean</i>	2.5%	97.5%	<i>mean</i>	2.5%	97.5%
First-year	0.30	0.19	0.43	0.01	0.00	0.01
Adult (R)	0.67	0.56	0.77			
Adult (NR)	0.33	0.22	0.47			
Adult ♂				0.01	0.01	0.02
Adult ♀				0.03	0.02	0.05
Recovery probability	<i>mean</i>	2.5%	97.5%	<i>mean</i>	2.5%	97.5%
First-year				0.01	0.00	0.01
Adult				0.04	0.03	0.05
Breeding probability	<i>mean</i>	2.5%	97.5%	<i>mean</i>	2.5%	97.5%
Ψ^j_{σ}	0.76	0.55	0.89	0.59	0.23	0.97
Ψ^j_{φ}	0.70	0.49	0.88	0.98	0.93	1.00
Ψ^a_{σ}	0.78	0.63	0.97	0.58	0.25	0.96
Ψ^a_{φ}	0.84	0.70	0.99	0.94	0.85	1.00
Breeding state certainty	<i>mean</i>	2.5%	97.5%	<i>mean</i>	2.5%	97.5%
d_{σ}	0.84	0.66	0.99	0.47	0.24	0.93
d_{φ}	0.85	0.71	0.99	0.75	0.70	0.83
Productivity	<i>mean</i>	2.5%	97.5%	<i>mean</i>	2.5%	97.5%
# of fledgings	0.55	0.27	0.87	0.46	0.26	0.72
p(hatching)				0.44	0.39	0.49
clutch size				3.64	3.54	3.87
chick survival				0.18	0.13	0.25
p(replacement clutch)				0.95	0.82	1.00
Immigration	<i>mean</i>	2.5%	97.5%	<i>mean</i>	2.5%	97.5%
# of immigrants	3.48	0.85	4.95			

figure legends

567 **Figure 1:** Posterior mean and 95% credible intervals of population size and demographic rates of the lapwing breeding populations in the Schleswig-Holstein region in Germany, from 2007 to 2016, and in the Netherlands, from 1995 to 2015. A and B: Estimates of
570 annual population index. The predicted and observed population indexes are shown in black and grey, respectively. C and D: Estimates of annual index of yearlings recruited by the population (open circles), of adults (filled circles) and of immigrants (triangles). E
573 and F: Annual first-year (open circles) and adult (filled circles) survival. G and H: Productivity (filled circles), hatching probability (open circles) and chick survival (triangles). I and J: Annual population growth rates.

576 **Figure 2:** Prospective and retrospective analyses. A and B: Elasticities of the population growth rate to the demographic rates in both populations. C and D: Contributions of the temporal variability of each demographic rate to the temporal variation in the re-
579 alized population growth rate. H : hatching probability; S^c : chick survival; E: clutch size, R: probability of laying a replacement clutch; P: productivity; Ψ^j : first-year breeding probability, Ψ^a : adult breeding probability, S^j : first-year survival, S^a : adult survival,
582 I : immigration, N^j : number of first-year individuals, N^a : number of adult individuals. Demographic rates shared by both populations are shown in grey.

Figure 3: 95% credible intervals of the predicted population indexes of the breeding pop-
585 ulations of lapwings in the Schleswig-Holstein region and in the Netherlands until 2030. Predictions of population indexes from the IPMs included year as random effects on the different demographic rates. Horizontal black dashed lines show when populations fall
588 below 5% of their size in the first year of the studied period.

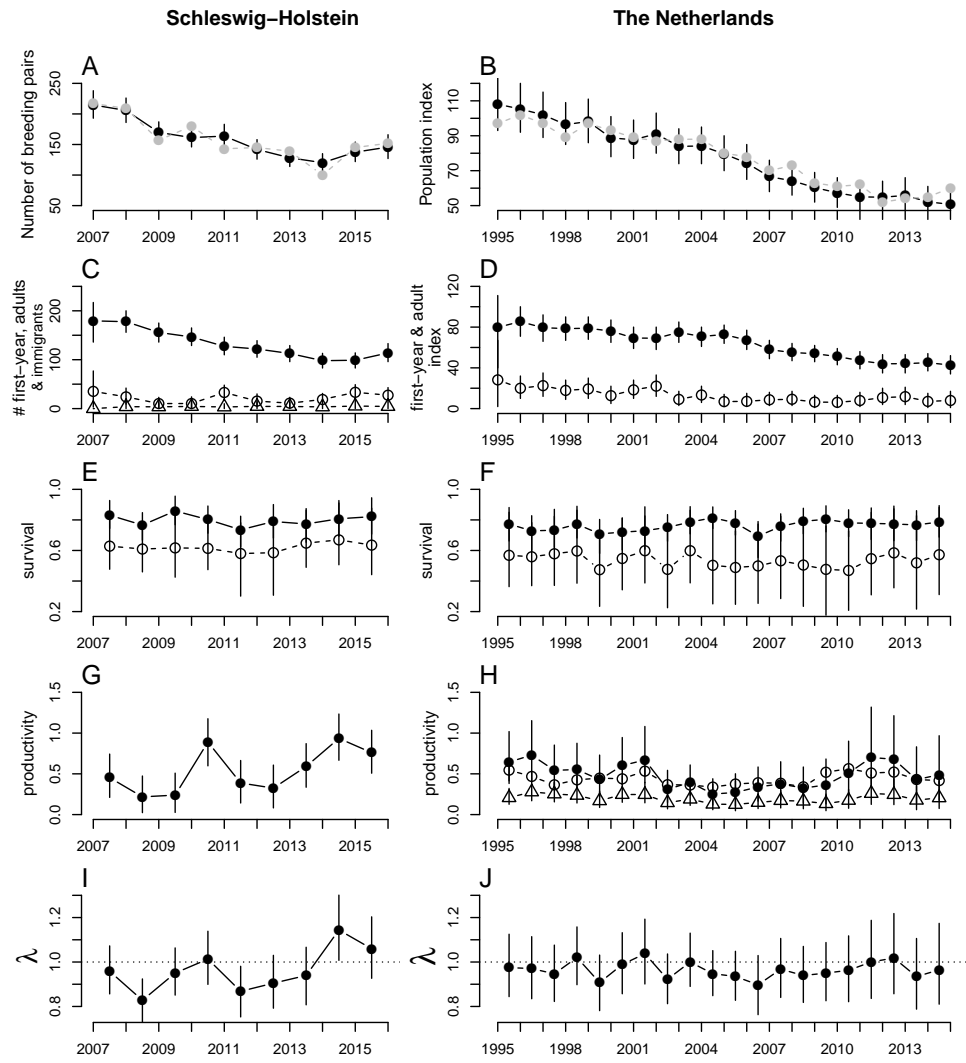


Figure 1

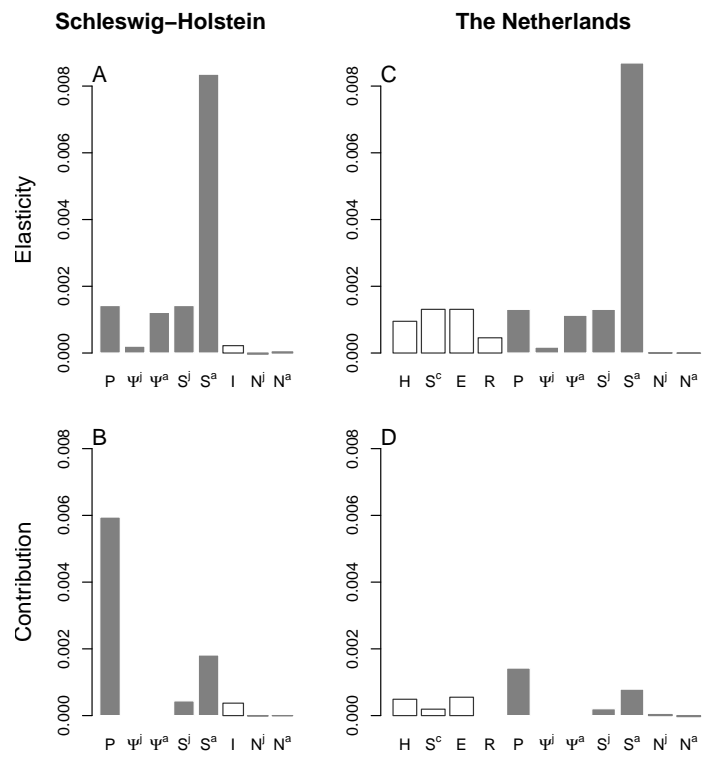


Figure 2

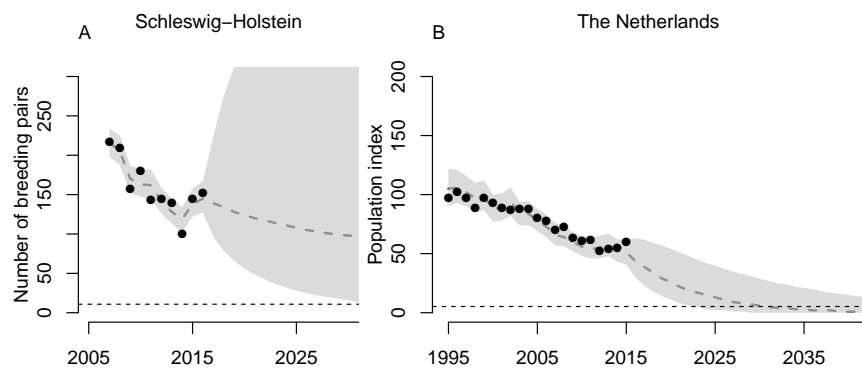


Figure 3

Online Supplementary material: Integrated Population Models

We developed pre-breeding models with 2 ages: First-year and adult birds. The state
591 process describing the dynamic of the population used matrix projection models:

SH:

$$\begin{bmatrix} N_{t+1}^j \\ N_{t+1}^a \end{bmatrix} = \begin{pmatrix} \Psi^j \frac{P_t}{2} S_t^j & \Psi^a \frac{P_t}{2} S_t^j \\ S_t^a & S_t^a \end{pmatrix} \begin{bmatrix} N_t^j \\ N_t^a \end{bmatrix} + \begin{bmatrix} 0 \\ I_t \end{bmatrix}$$

NL:

$$\begin{bmatrix} N_{t+1}^j \\ N_{t+1}^a \end{bmatrix} = \begin{pmatrix} \Psi^j \frac{1}{2} [1 + (1 - H_t)R] * E_t H_t S_t^c S_t^j & \Psi^a \frac{1}{2} [1 + (1 - H_t)R] * E_t H_t S_t^c S_t^j \\ S_t^a & S_t^a \end{pmatrix} \begin{bmatrix} N_t^j \\ N_t^a \end{bmatrix}$$

where N_t^j and N_t^a are the annual indexes of first-year and adult individuals, S_t^j and
 S_t^a are the annual first-year and adult survival, Ψ^j and Ψ^a are the breeding probabilities
594 of first-year and adult birds, and P_t is the annual productivity defined as the annual
number of fledglings produced per female. We assumed an even sex ratio and divided
the productivity by two to retain only females in the model. In NL, the productivity was
597 decomposed into the different components clutch size (E_t), hatching probability (H_t),
chick survival (S_t^c), and probability of reneating if the first clutch has failed (R). In NL,
we assumed no immigration because the population has a large spatial scale.

600 Survival

Because of the uncertainty about the breeding status of some individuals in both popu-
lations, we used a multi-event model to analyze jointly first-year and adult survival and
603 breeding probabilities. In NL, chick survival was also estimated. We had two observa-

tions to describe a captured bird: breeding (if the bird was captured on the nest in NL or, if the bird was observed with courtship, nesting or territoriality behaviour in SH) or unknown breeding state (all other observations). Here we present the models in terms of matrices for each population:

Model for Schleswig-Holstein

4 observations (J: Juvenile, B: Breeder, U: Breeding status unknown, 0: not captured)

4 states (J: Juvenile, B: Breeder, NB: Non-breeder, D: Dead)

$$\text{Probability in first capture: } \begin{matrix} & J & B & U & 0 \\ \begin{bmatrix} 1 & 1 & 0 & 0 \end{bmatrix} \end{matrix}$$

the state of each bird was known when it was marked either as chick or as breeder.

$$\text{Transition matrix: } \begin{matrix} & J & B & NB & D \\ \begin{matrix} J \\ B \\ NB \\ D \end{matrix} \begin{bmatrix} 0 & S^j \Psi_{sex}^j & S^j (1 - \Psi_{sex}^j) & 1 - S^j \\ 0 & S^a \Psi_{sex}^a & S^a (1 - \Psi_{sex}^a) & 1 - S^a \\ 0 & S^a \Psi_{sex}^a & S^a (1 - \Psi_{sex}^a) & 1 - S^a \\ 0 & 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

$$\text{Recapture Matrix: } \begin{matrix} & J & B & U & 0 \\ \begin{matrix} J \\ B \\ NB \\ D \end{matrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & d_{sex} p_{age} & (1 - d_{sex}) p_{age} & 1 - p_{age} \\ 0 & 0 & p_{age} & 1 - p_{age} \\ 0 & 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

where d is the probability of correctly assigning the breeding state and p is the recapture probability

Goodness of fit We evaluated the overall goodness of fit to the SH data of a Cormack-Jolly-Seber model with two age classes using U-CARE (Choquet *et al.*, 2009). This test

revealed trap-happiness in the data ($\chi^2 = 31.39, df = 6, p < 0.01$) probably because the recapture were re-sightings based on the observations of color ringed birds on known territories. The other components of the goodness-of-fit test were not significant ($p > 0.39$). The recapture probabilities in SH were thus modeled with an age effect (first-year vs. after first year recapture) and trap-happiness. In a given year, the trap happiness assumed that the birds captured in the previous year had a higher probability to be recaptured than the birds that have not been captured in the previous year. A pre-analysis of annual survival revealed that no difference between male and female survival could be detected (sex effect: -0.05 [-0.81;0.86]) and annual survival was modeled with an age-effect, only.

Model for The Netherlands

7 observations (N: Chick, J: Juvenile, B: Breeder, U: Breeding status unknown, RF: ringed as chick and recovered dead before fledging, R: recovered dead after fledging, 0: not captured). N and J were set according to the age in the Euring Code (N: Age 1, J: Age 2 or 3: fully grown or fledged bird).

7 states (N: Chick, J: Juvenile, B: Breeder, NB: Non-breeder, Y: recently dead, YF: recently dead before fledging, D:Dead)

Probability in year of first capture:

$$\begin{matrix} & N & J & B & U & RF & R & 0 \\ \left[\begin{array}{ccccccc} S^c + (1 - S^c)(1 - r_{age}) & 1 & \Psi_{sex}^a d_{sex} & \Psi_{sex}^a * (1 - d_{sex}) + (1 - \Psi_{sex}^a) & (1 - S^c)r_{age} & 0 & 0 \end{array} \right] \end{matrix}$$

The state was unknown for most birds in their first capture. For adults, the breeding status was unknown for some of them. For birds marked as chicks, we did not know if they have died before or after fledging if they have not been recaptured in the following

years. Thus, chick survival (S^c , the probability to survive from chicks to fledging) was
 642 estimated using the capture histories of the birds first captured as chicks and the chicks
 recovered dead before fledging during their first year of capture.

$$\text{Transition Matrix: } \begin{array}{c} N \\ J \\ B \\ NB \\ YF \\ Y \\ D \end{array} \begin{array}{c} N \\ J \\ B \\ NB \\ YF \\ Y \\ D \end{array} \begin{bmatrix} 0 & 0 & S^j \Psi_{sex}^j & S^j(1 - \Psi_{sex}^j) & 0 & 1 - S^j & 0 \\ 0 & 0 & S^j \Psi_{sex}^j & S^j(1 - \Psi_{sex}^j) & 0 & 1 - S^j & 0 \\ 0 & 0 & S^a \Psi_{sex}^a & S^a(1 - \Psi_{sex}^a) & 0 & 1 - S^a & 0 \\ 0 & 0 & S^a \Psi_{sex}^a & S^a(1 - \Psi_{sex}^a) & 0 & 1 - S^a & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

$$\text{Recapture Matrix: } \begin{array}{c} N \\ J \\ B \\ NB \\ YF \\ Y \\ D \end{array} \begin{array}{c} N \\ J \\ B \\ NB \\ YF \\ Y \\ D \end{array} \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & d_{sex} p_{sex} & (1 - d_{sex}) p_{sex} & 0 & 0 & 0 & 1 - p_{sex} \\ 0 & 0 & p_{sex} & 0 & 0 & 0 & 1 - p_{sex} \\ 0 & 0 & 0 & 0 & r_{age} & 0 & 1 - r_{age} \\ 0 & 0 & 0 & 0 & 0 & r_{age} & 1 - r_{age} \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

where d is the probability of correctly assigning the breeding state, p is the recapture
 probability and r is the recovery probability.

648 **Goodness of fit** We used the Goodness of fit for the combined recapture and recovery
 data derived by McCrea, Morgan & Pradel (2014) to test the homogeneity of our data
 including only birds older than 1 year. Test 2 was not significant ($\chi^2 = 55.71$, $df = 74$,

651 $p = 0.94$) but Test 3 was (3.sv: $\chi^2 = 120.28$, $df = 19$, $p < 0.001$, 3.sd: $\chi^2 = 0.31$, $df = 11$,
654 $p > 0.999$ and 3.smd: $\chi^2 = 362.91$, $df = 18$, $p < 0.001$) indicating an additional age effect
among adults older than one year or possible transience in this population. However,
654 because we did not have additional information about the age of the birds, survival
was modeled with a two age classes (first year vs. adult) and no sex differences. A
preliminary model revealed that there was no difference of survival between sexes (sex
657 effect: 0.14 [-0.25;0.57]). Recapture probabilities were modeled by including an effect
of sex because females were easier to capture when they were on the nest than males
(sex effect: 1.40 [1.03;1.07]). We also included an age effect in recapture probabilities.
660 Because first-year individuals tend to migrate further and may suffer different sources of
mortality than adults, recovery probability included an age but no sex effect.

Table S1: Posterior means with associated standard deviations and 95% credible intervals of the parameters from the IPMs describing the dynamics of the lapwing populations in Schleswig-Holstein and in the Netherlands. The estimates for the intercepts (*int*) and the standard deviations of the random effects of year (σ^t) are presented on the logit scale for survival, recapture, recovery and, hatching probabilities. The probabilities of recapture of adult birds that have been captured or not in the previous year in the population of Schleswig-Holstein are noted (*R*) and (*NR*), respectively.

	Schleswig-Holstein				Netherlands			
	<i>mean</i>	<i>SD</i>	2.5%	97.5%	<i>mean</i>	<i>SD</i>	2.5%	97.5%
First-year survival probability (logit scale)								
<i>int</i>	0.52	0.35	-0.05	1.33	0.16	0.38	-0.47	1.01
σ^t	0.37	0.38	0.01	1.40	0.48	0.36	0.02	1.35
Adult survival probability (logit scale)								
<i>int</i>	1.44	0.24	1.03	2.00	1.19	0.12	0.98	1.45
σ^t	0.46	0.32	0.03	1.24	0.33	0.14	0.06	0.64
Recapture probability (logit scale)								
<i>int</i> first-year	-0.85	0.29	-1.43	-0.27	-4.94	0.28	-5.51	-4.40
<i>int</i> adult (<i>R</i>)	0.71	0.24	0.24	1.20				
<i>int</i> adult (<i>NR</i>)	-0.72	0.29	-1.29	-0.14				
<i>int</i> adult σ					-4.56	0.22	-5.00	-4.15
<i>int</i> adult φ					-3.34	0.18	-3.72	-2.99
σ_p^t	0.58	0.23	0.26	1.13	0.71	0.16	0.45	1.09
Recovery probability (logit scale)								
<i>int</i> first-year					-5.14	0.14	-5.43	-4.87
<i>int</i> adult					-3.17	0.15	-3.47	-2.88
σ^t					0.47	0.11	0.29	0.73
Breeding probability (natural scale)								
$\Psi^j \sigma$	0.76	0.09	0.55	0.89	0.59	0.21	0.23	0.97
$\Psi^j \varphi$	0.70	0.10	0.49	0.88	0.98	0.02	0.93	1.00
$\Psi^a \sigma$	0.78	0.10	0.63	0.97	0.58	0.20	0.25	0.96
$\Psi^a \varphi$	0.84	0.08	0.70	0.99	0.94	0.04	0.85	1.00
Breeding state certainty (natural scale)								
d_σ	0.84	0.09	0.66	0.99	0.47	0.19	0.24	0.93
d_φ	0.85	0.08	0.71	0.99	0.75	0.03	0.70	0.83
Number of fledglings (natural scale)								
<i>int</i>	0.55	0.16	0.27	0.87				
σ^t	0.37	0.12	0.19	0.67				
σ^{site}	0.40	0.48	0.06	1.55				
σP	1.12	0.23	0.77	1.65				
Hatching probability (logit scale)								
<i>int</i>					3.58	0.07	3.44	3.72
σ^t					0.23	0.05	0.16	0.34
<i>protection</i>					0.40	0.05	0.30	0.51
Chick survival probability (logit scale)								
<i>int</i>					-1.49	0.21	-1.91	-1.08
σ^t					0.50	0.20	0.12	0.93
Immigration								
<i>int</i>	3.48	1.15	0.85	4.95				
σ^{int}	2.24	2.09	0.05	7.82				

Table S2: Prior sensitivity analysis on the IPM in SH. Posterior means with associated standard deviations and 95% credible intervals of the parameters from the IPMs describing the dynamics of the lapwing populations in Schleswig-Holstein. We used different prior distributions for Ψ . Prior 1: uniform distribution on the intervals [0.1;0.9] and [0.6;1] for first-year and adult individuals. Prior 2: uniform distributions on the interval [0;1] for both age classes. This corresponds to a non-informative prior. Prior 3: beta distribution with shape parameters 5 and 8, and 11 and 6 for first-year and adult individuals, respectively.

prior on Ψ	Prior 1				Prior 2				Prior 3			
	<i>mean</i>	<i>SD</i>	2.5%	97.5%	<i>mean</i>	<i>SD</i>	2.5%	97.5%	<i>mean</i>	<i>SD</i>	2.5%	97.5%
First-year survival												
<i>int</i>	0.523	0.349	-0.048	1.333	0.528	0.368	-0.024	1.269	0.580	0.368	-0.008	1.439
σ^t	0.372	0.380	0.010	1.402	0.378	0.436	0.013	1.361	0.414	0.429	0.014	1.519
Adult survival												
<i>int</i>	1.437	0.244	1.033	2.002	1.421	0.268	1.006	2.028	1.444	0.252	1.040	2.045
σ^t	0.464	0.321	0.034	1.242	0.460	0.343	0.035	1.302	0.455	0.306	0.037	1.216
Recapture probability												
<i>int</i> first-year	-0.849	0.290	-1.425	-0.274	-0.843	0.293	-1.421	-0.269	-0.872	0.302	-1.471	-0.283
<i>int</i> adult (R)	0.707	0.242	0.237	1.203	0.718	0.242	0.252	1.219	0.701	0.247	0.222	1.197
<i>int</i> adult (NR)	-0.718	0.293	-1.292	-0.143	-0.707	0.289	-1.270	-0.117	-0.746	0.300	-1.343	-0.154
σ_p^t	0.578	0.227	0.264	1.131	0.578	0.226	0.264	1.138	0.584	0.239	0.266	1.162
Breeding probability												
Ψ^j_{σ}	0.759	0.093	0.550	0.893	0.692	0.135	0.438	0.955	0.528	0.085	0.363	0.694
Ψ^j_{φ}	0.701	0.103	0.492	0.880	0.814	0.102	0.606	0.986	0.641	0.073	0.495	0.779
Ψ^a_{σ}	0.780	0.095	0.625	0.974	0.821	0.103	0.633	0.991	0.715	0.060	0.608	0.840
Ψ^a_{φ}	0.839	0.082	0.702	0.989	0.838	0.080	0.701	0.984	0.747	0.041	0.678	0.839
Breeding state certainty												
d_{σ}	0.841	0.093	0.661	0.991	0.802	0.102	0.628	0.987	0.910	0.065	0.764	0.997
d_{φ}	0.852	0.083	0.708	0.992	0.850	0.080	0.710	0.990	0.944	0.043	0.842	0.998
Number of fledglings												
<i>int</i>	0.551	0.155	0.268	0.871	0.537	0.160	0.241	0.881	0.565	0.159	0.274	0.901
σ^t	0.371	0.124	0.193	0.671	0.348	0.124	0.184	0.664	0.342	0.118	0.182	0.627
σ^{site}	0.399	0.484	0.056	1.550	0.404	0.520	0.056	1.597	0.429	0.539	0.053	1.742
σ^P	1.116	0.227	0.773	1.647	1.118	0.232	0.775	1.677	1.123	0.235	0.778	1.677
Immigration												
<i>int</i>	3.482	1.148	0.849	4.947	3.449	1.137	0.899	4.937	3.500	1.145	0.873	4.948
σ_i	2.237	2.090	0.053	7.823	2.026	1.918	0.053	7.720	2.228	2.131	0.069	8.406

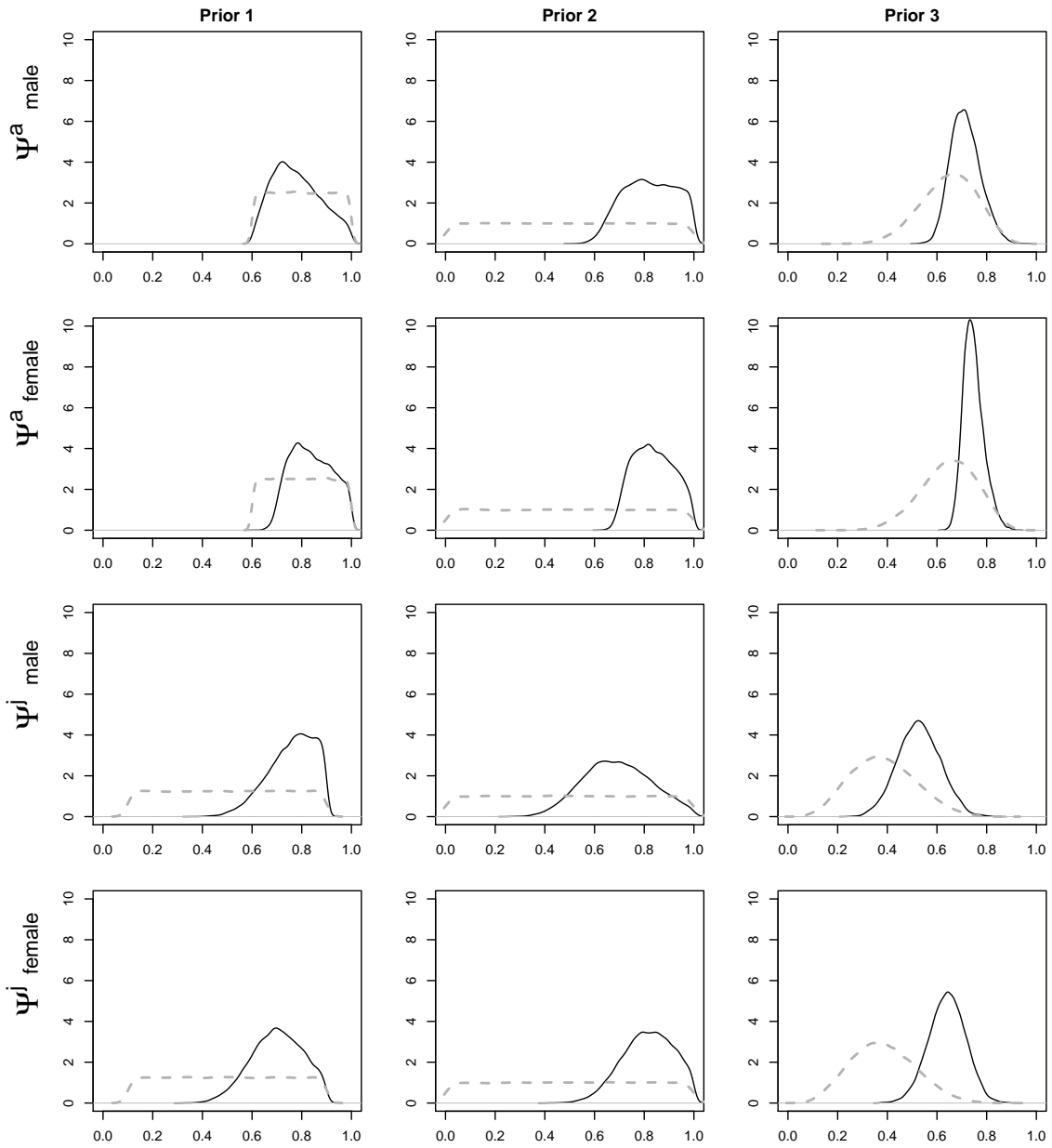


Figure S1: Posterior distribution of breeding probabilities (black lines) in the lapwing population in SH when using 3 different prior distributions (dashed grey lines). Prior 1 is $U(0.1;0.9)$ and $U(0.6;1)$ for first-year and adult breeding probabilities. Prior 2 is $U(0;1)$ for breeding probabilities of both age classes. Prior 3 is $Beta(5,8)$ and $Beta(11,6)$ for first-year and adult breeding probabilities