Seasonal changes in distribution and abundance of a local Corncrake population

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Abstract

Many bird species have experienced short- or long-term population declines. However, the mechanisms and reasons underlying such negative changes are often not fully understood, making it difficult to identify effective conservation measures to recover populations. In this study, we focused on local changes in the abundance and distribution of calling male Corncrakes *Crex crex* in relation to: (1) within- and between-season site fidelity of adult males, (2) spatial distribution of territories in consecutive years and (3) the effect of habitat conditions on population size. We counted the number of calling males at ten randomly selected study plots (1 km²) in 2014–2018. Additionally, males were caught and individually marked in years 2015–2017. We found significant between-year changes in Corncrake abundance, from a 34% decrease to a 21% increase. On average, 32% of males established territories in the same locations as males recorded in the previous year. Breeding site fidelity was very low, with only 2–5% of males recaptured in the following year. Males selected areas characterized by higher values of NDVI (Normalized Difference Vegetation Index—higher values indicate more biomass) than on average within the study area. Population size in a particular year was significantly affected by the NDVI of the previous year but not by the NDVI in the current breeding season. We suppose that Corncrakes may exhibit a nomadic breeding behavior, and settle at territories when they encounter optimal habitat conditions. Moreover, as population size was negatively correlated with habitat conditions at the beginning of the previous breeding season, we suppose that local population changes may reflect more general trends in a whole population rather than local breeding success. Therefore, we highlight the need for better knowledge of Corncrake dispersal within the main European population and for the coordination of monitoring and conservation efforts, especially in those regions where most Corncrakes breed.

Keywords Census · Population trend · Local population · Site fidelity · Dispersion · Nomadic breeding behavior

Zusammenfassung

Jahreszeitliche Veränderungen in Verbreitung und Häufigkeit einer lokalen Wachtelkönig-Population

Viele Vogelarten haben kurz- oder langfristige Populationsabnahmen durchlebt. Allerdings sind die Mechanismen und Ursachen, welche solchen negativen Entwicklungen zugrunde liegen, nicht erschöpfend erforscht, was die Festlegung

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wirksamer Schutzmaßnahmen zur Wiederherstellung der Populationen erschwert. In dieser Untersuchung konzentrierten wir uns auf lokale Veränderungen in Häufigkeit und Verbreitung rufender Wachtelkönig-Männchen *Crex crex* im Verhältnis zu 1) Ortstreue adulter Männchen innerhalb einer sowie zwischen den Brutsaisons, 2) die räumliche Verteilung der Reviere in aufeinanderfolgenden Jahren sowie 3) Auswirkungen der Lebensraumbedingungen auf die Populationsgröße. Wir erfassten die Anzahl rufender Männchen auf zehn zufällig ausgewählten Untersuchungsflächen (1 km²) in den Jahren 2014–2018. Zusätzlich wurden zwischen 2015–2018 Männchen gefangen und individuell markiert. Wir stellten signifikante Unterschiede in der Häufigkeit von Wachtelkönigen zwischen den einzelnen Jahren fest, von einer 34%-igen Abnahme bis hin zu einem Anstieg um 21%. Im Schnitt besetzten 32% der Männchen Reviere an denselben Orten wie die im Vorjahr festgestellten Männchen. Die Brutplatztreue lag sehr niedrig, und nur 2–5% der Männchen wurden im Folgejahr wiedergefangen. Die Männchen wählten Bereiche mit höheren NDVI-Werten (engl.: Normalised Difference Vegetation Index; Normalisierter Differenzen-Vegetations-Index; höhere Werte zeigen mehr Biomasse an) als der Durchschnitt innerhalb des Untersuchungsgebietes. Die Populationsgröße in einem gegebenen Jahr wurde signifikant durch den NDVI-Wert des Vorjahres beeinflusst, nicht jedoch durch den NDVI-Wert der laufenden Brutsaison. Wir vermuten, dass Wachtelkönige ein nomadisches Brutverhalten zeigen und sich in Revieren ansiedeln, in denen sie optimale Bedingungsverhältnisse vorfinden. Da zudem die Populationsgröße negativ mit den Lebensraumbedingungen zu Beginn der vorangegangenen Brutsaison korrelierte, nehmen wir weiterhin an, dass lokale Populationsveränderungen vermutlich eher allgemeine Trends in der Gesamtpopulation widerspiegeln als lokale Bruterfolge. Daher möchten wir auf den Bedarf an zusätzlichen Erkenntnissen über Dismigration bei Wachtelkönigen innerhalb der europäischen Hauptpopulation sowie an einer Koordination von Erfassungs- und Schutzmaßnahmen hinweisen, speziell in den Regionen, in denen die meisten Wachtelkönige brüten.

Introduction

In Europe, many bird species, including both common and widespread (Inger et al. 2015) as well as rare and endangered ones (Colhoun et al. 2015) have experienced long-term population declines and decreased geographical distributions (Reif et al. 2008; Inger et al. 2015). The intensity of these negative changes varied in time and was different in Western and Eastern Europe (Reif and Vermouzek 2019; Reif et al. 2008; Tryjanowski et al. 2011). The main factors responsible for population decline appear to be related to human activity such as agricultural intensification (Reif et al. 2008), human-induced climate changes (Virkkala and Rajasärkkä 2011), pollution (Goulson 2014), hunting (Székely and Sutherland 2010) and habitat fragmentation or loss (Schmiegelow and Mönkkönen 2002). Simultaneously, looking at long-term trends, many bird species show yearly, local fluctuations (Sæther et al. 2016) caused by various extreme biotic and abiotic disturbances, which may have both immediate and long-lasting influences on population dynamics (Tryjanowski et al. 2009). Such short-term perturbations may be attributed to various food availability (Tryjanowski et al. 2009; Karell et al. 2009), the avoidance of nest predation (Szymkowiak and Kuczyński 2015), annual changes in the availability of ephemeral habitats (Tucker et al. 2004), rapid habitat loss (Zuckerberg and Vickery 2006), diseases or extreme weather conditions in breeding areas, migration routes and wintering grounds (Conrey et al. 2016; Becker and Finck 1985; Robinson et al. 2007). Ground-nesting species are particularly sensitive to fluctuations in water levels and vegetation structure and respond to these changes by shifting between breeding sites in optimal and sub-optimal

years, leading to annual fluctuations in abundance (Sharps et al. 2017; Shuford 2016; Lopes et al. 2015). However, local population changes may also come from a very specific, nomadic breeding strategy. In some polygynous species, males do not have a final breeding destination but visit many sites within a whole breeding range to increase the chances to reproduce (Kempenaers and Valcu 2017). As a consequence, both between- as well as a within-year variation in local population size can be considerable.

Regardless of whether population changes are rapid or gradual, successful management and conservation requires continuous monitoring of bird populations to determine, where possible, the factors responsible for the population decrease and so influence the conservation strategies. For migratory bird species conservation is challenging as unfavorable factors may influence the populations in various locations such as breeding areas (Mallord et al. 2016), migration routes (Hewson et al. 2016) and wintering grounds (Székely and Sutherland 2010). Therefore, the conservation and management of breeding habitats alone may be insufficient to maintain a population (Serra et al. 2015), or a population decline may be observed even when the breeding habitat remains unchanged. Moreover, even high productivity in a local population may be insufficient to stabilize their trend when the emigration rate is high (Dale and Steifetten 2011). Thus, understanding local population changes requires knowledge of site fidelity and dispersion pattern of the species. Without this knowledge, it is impossible to say whether local population changes are caused by low breeding success, changes of habitat quality, bird movement between subpopulations or other factors operating outside the breeding areas.

In this study, we focused on short-term changes in the abundance and distribution of a local Corncrake *Crex crex* population and on potential factors responsible for these fluctuations. The Corncrake is a long-distance migratory species. Birds from eastern European populations migrate across eastern Africa and overwinter in sub-Saharan Africa, mainly in the east (Walther et al. 2013). Existing data have not given much evidence that Corncrakes experience major threats in their African wintering range (Stowe and Becker 1992). However, hunting during migration (Baha el Din et al. 1996) and environmental changes in the wintering areas and at stop-over sites may become significant factors influencing the population dynamics and so will need careful monitoring (Walther et al. 2013).

In breeding areas Corncrakes occupy a variety of open habitats, including grasslands, arable fields, meadows, pastures, and unmanaged areas (Berg and Gustafson 2007; Budka and Osiejuk 2013; Dorresteijn et al. 2015). Birds prefer tall (> 20 cm) but not extremely dense vegetation (Schäffer 1997; Michalska-Hejduk et al. 2017). At the beginning of the breeding season, the probability of Corncrake occurrence is positively affected by the presence of shrubs, patches of abandoned meadows or meadows unmown in the previous year (Budka and Osiejuk 2013).

For many years, the Corncrake population was in decline, especially in Western Europe, and the species was classified as endangered (Green et al. 1997). In the 1980s, a dramatic population fall (30% on average) was observed in Britain and Ireland (Stowe et al. 1993). More recent results of Corncrake monitoring indicate pronounced annual fluctuations in abundance in many countries, including persistent declines in the west and south and stable populations in the east (Koffijberg et al. 2016). The main factors responsible for the Corncrake population changes appeared to be agricultural intensification, mechanized mowing early in the breeding season, and the loss of suitable breeding habitats (Green et al. 1997; Koffijberg and Schäffer 2006). Many countries have implemented various conservation plans to protect the Corncrake and counteract the unfavorable population trends of this species (O'Brien et al. 2006; Wilkinson et al. 2012; Inderwildi and Müller 2015; Bellebaum and Koffijberg 2018). Conservation activities and changes in agriculture, particularly in the eastern part of the species range, seem to have reversed the Corncrake's decline (Koffijberg and Schäffer 2006) and according to the IUCN listings, the species is currently classified as being of "least concern" globally with a stable population trend (BirdLife International 2016). However, currently, in many European countries large annual fluctuations of the Corncrake population are observed and the factors responsible for these fluctuations are insufficiently examined (Koffijberg et al. 2016). Therefore, conservation biologists should carefully monitor long-term population trends of the Corncrake. Such coordinated population and habitat

change monitoring is especially required for the central and eastern range of the species, where six countries (Russia, Ukraine, Romania, Belarus, Poland and Latvia) hold more than 90% of the European Corncrake population (Koffijberg et al. 2016).

Many studies have focused on habitat preferences and the response of Corncrakes to various habitat management regimes on the breeding grounds and so we have a good understanding of the conservation measures needed to ensure optimal habitat conditions for Corncrakes (see review in Koffijberg and Schäffer 2006). One challenge is that our understanding of Corncrake site fidelity and dispersal remains incomplete. In Scotland, the annual survival rate of adult male Corncrakes was very low (0.2–0.3) in comparison to other bird species (Green 2004). Most adult males return to within 1 km of the ringing site and only 6% disperse further than 10 km in the next year after ringing (Green 1999). On the other hand, in continental Europe, long-distance movements (more than 1 000 km) within a breeding season have been observed (Koffijberg et al. 2016). Unfortunately, the survival rate of birds from the continental population is unknown. Therefore, we do not know whether Corncrakes experience high mortality during migration and wintering, or alternatively, that their low site fidelity is related to a nomadic breeding behavior in the breeding grounds. Without this knowledge, it is difficult to identify the factors responsible for population changes, especially when a breeding habitat seems to be locally stable. In addition, the Corncrake population, like other migratory bird species, may show a decline because of changes in habitat quality along migration routes or in overwintering areas but not as a consequence of local breeding habitat change. The recognition of exact migration routes, important stop-over sites and environmental changes in wintering areas is another challenge necessary to provide effective population management (Walther et al. 2013).

In this study, we examined local changes in the abundance and spatial distribution of calling male Corncrakes across five consecutive breeding seasons. To better understand the factors responsible for population changes, we determine whether (1) adult males return to the same breeding population in the following year, (2) whether territories are established in the same locations in different years, (3) if males occupy territories in places with denser vegetation than in surrounding areas, and (4) whether habitat conditions in the current or previous season explain changes in annual Corncrake abundance. We discuss our results in the context of the conservation and management of Corncrake populations.

Materials and methods

Study area

We conducted our study in extensively managed farmland of the Upper Nurzec River Valley (52°36'N, 23°14'E)—an area in eastern Poland of international importance for birds (IBA PL056), protected as Nature 2000 (Dolina Górnego Nurca PLB200004; Ostoja w Dolinie Górnego Nurca PLH200021). It is home to breeding populations of Corncrake (206–229 calling males), Montagu's Harrier *Circus pygargus* (9–18 breeding pairs), Black-tailed Godwit *Limosa limosa* (13–31 breeding pairs), Northern Lapwing *Vanellus vanellus* (50–63 breeding pairs), Eurasian Curlew *Numenius arquata* (2–5 breeding pairs), and Great Grey Shrike (6–7 breeding pairs) (Wilk et al. 2010). The study area spans approximately 46 km² of drained meadows, grasslands, pastures, abandoned meadows, agricultural fields and forests. Forests and agricultural fields are located around the valley edges and cover ca 17% and ca 7% of the study area, respectively. Pastures are located near to the villages and cover ca 2% of the study site. Shrubs mainly grow along the water channels or at low densities in unmanaged meadows. Meadows

cover ca 70% of the study area, of which most (ca 60%) are managed under various agri-environmental schemes and are mowed once or twice in July/August. Approximately, 20% of meadows are mowed irregularly and are undergoing various stages of succession, while the remaining area is managed intensively and mowed two–three times per year, from the end of May to the end of September. Floods are brief, rare, and affect only the land closest to the river (Budka and Osiejuk 2013). During the study period, we did not observe any considerable changes in land use or intensity of mowing.

Distribution, abundance and site fidelity of male Corncrakes

To sample the population of Corncrakes, we randomly selected ten 1 × 1 km study plots from those in which forests covered less than 20% (Fig. 1). The study plots were surveyed from 27 May to 4 June 2014–2018. The turn of May and June is the peak period of calling by male Corncrakes in Poland (Schäffer 1997). During this period, unpaired males occupy territories and utter calls almost continuously (ca. 90% of nocturnal activity; Tyler and Green 1996). Therefore, a single survey of the study area at this time should allow for

Fig. 1 Map showing the location of the study area and ten randomly selected study plots (1 × 1 km)

the detection of around 80–90% of males present within the study plots (Tyler and Green 1996).

Male Corncrakes are vocally active at night. During the breeding season, they produce a loud (90–100 dB at 1 m; Rek and Osiejuk 2013), disyllabic crackling call which can be heard up to 1 km away (Schäffer and Koffijberg 2004). We conducted our surveys at night, from 22:00 to 3:00 (local time). We censused Corncrakes using territory mapping, which seems to be the most accurate method of monitoring populations of this species (Budka and Kokociński 2015). Study plots were surveyed by walking transects up to 500 m apart. This design allowed us to hear calling males from distances of less than 250 m, which meant that the probability of missing a calling male was very low. On hearing a calling male, observers approached the bird and recorded its position using a GPS receiver. Approaching the birds did not cause them to move; observers stopped approaching the birds when they stopped calling or when we were around 5 m away. Consequently, the spatial locations of the calling males were determined with an accuracy of a few meters (accuracy of the GPS receiver combined with the distance between the receiver and the bird).

Additionally, in 2015–2017, we captured calling males and marked them using alphanumeric metal bird rings. We tried to catch all of the calling males within the same ten study plots at which males were counted, including a buffer area of up to ca 100 m around each plot. The catching of birds was undertaken between one and four nights after counts were made at each study plot. Territorial males were lured by playback and caught with a hand-net. Additionally, in 2017, we made a second visit to catch birds to investigate within-season territory fidelity. Visits were made between 4 and 12 June to the same locations at which birds were caught during the first visit. We occasionally observed mowing between visits. We were unable to catch all males in each year because 5–10% of them did not approach the speaker.

Habitat conditions

To characterize habitat conditions, we calculated a Normalized Difference Vegetation Index (NDVI) (Rouse et al. 1973) based on Landsat 8 satellite images (30-m resolution in multispectral bands; retrieved from <https://earthexplorer.usgs.gov>). This index (Eq. 1) is commonly used to assess the vegetation density and the photosynthetic activity of plants. The NDVI is correlated with several biophysical parameters of the vegetation such as leaf area index, biomass and fractional vegetation cover (Jiang et al. 2006). The higher NDVI values (NDVI ranges from -1 to 1) indicate greater levels of photosynthetic activity. Thus, NDVI will be low for areas of bare soil, moderate for sparse vegetation (shrubs, grasslands) and high for forest (Fung and Siu 2000). From the Corncrake perspective, this means that areas with higher values

of NDVI are covered by taller and more dense vegetation (which is preferred by Corncrakes; (Schäffer 1997; Michalska-Hejduk et al. 2017) and the proportion of vegetation-free areas (e.g., mowed meadows) is lower.

$$\text{NDVI} = \frac{R_{\text{NIR}} - R_{\text{RED}}}{R_{\text{NIR}} + R_{\text{RED}}} \quad (1)$$

Equation 1 NDVI calculation; R_{NIR} —reflectance in near-infrared band (wavelength 0.851–0.879 μm , band no. 5 in Landsat 8); R_{RED} —reflectance in red band (wavelength 0.636–0.673 μm , band no. 4 in Landsat 8).

The NDVI was calculated for two periods in each year of the study: the beginning of May (target date: 5th May) and June (target date: 10th June). These dates correspond with (1) the occupancy of territories by males after arrival from wintering grounds; and (2) egg-laying and incubation by females (Schäffer 1997). Unfortunately, Landsat 8 has its own schedule of flights and considering the low revisit time (8 or 16 days), it was not possible that every image could be acquired exactly on these dates. We were able to obtain data for the following dates: 5th May and 6th June 2013, 5th May and 16th June 2014, 2nd May and 12 June 2015, 4th May and 5th June 2016, 7th May and 8th June 2017 and 3rd May and 4th June 2018. Another obstacle in obtaining high-quality images for the study area was the cloud cover that frequently disturbs satellite scenes in temperate climates. To remove pixels covered by clouds and their shadows from the analysis, we used their mask included in every Landsat 8 scene (BQA band). To maximize efficiency in removing low-quality pixels, we also applied the cloudMask and cloudShadowMask methods described in Leutner et al. (2019). The cloudMask method relies on the substantial difference in reflectance between the blue (short-wave) and thermal (long-wave) bands, while the cloudShadowMask method relies on shifting the clouds to the shadow direction by an appropriate vector. Finally, we also removed a 3-pixel buffer around the removed cloud and shadow pixels. Seven scenes used in this study (~58%) showed clear-sky or less than 5% of cloud cover over the study area. The remaining five scenes (two in 2014, two in 2017 and in May 2015) were severely affected by clouds covering 34.5, 67.1, 72.4, 78.3 and 100% of the study area. In the first four images, where part of the data was of good quality, we used an Optical Cloud Pixel Recovery method (Tahsin et al. 2017) to estimate the NDVI values in places masked by clouds and shadows. Specifically, we extracted good-quality NDVI values as the dependent variable and developed random forest (RF) regression models using data from two clear-sky images (22 bands = 22 variables; centered and scaled) from the same year as independent variables. For this analysis, we used images acquired on 24th May 2014 and 3rd August 2014 for modeling NDVI on 16th June, 9th April 2015 and

12th June 2015 for modeling NDVI on 2nd May 2015, 4th April 2017 and 23rd May 2017 for modeling NDVI on 7th May 2017, 23rd May 2017 and 7th July 2017 for modeling NDVI on 8th June 2017. A repeated k-fold cross-validation was used to fit the RF models. RF model performance was assessed by root mean square error (RMSE) that reached between 0.032 and 0.055 depending on the proportion of good-quality data. Then, the NDVI was predicted by RF models in places covered by clouds. However, at the beginning of May 2014, the study area was entirely covered by dense clouds, so we were not able to obtain the dependent variable. In this case, we calculated the NDVI values on 22 April and 24 May 2014, when the sky was clear and linearly interpolated NDVI obtaining values on 5th May 2014. All the processing and calculations were performed in R software (R Core Team 2020) using the following packages: *caret* (Kuhn 2008), *raster* (Hijmans 2017) and *RStoolbox* (Leutner et al. 2019).

Data analysis

We compared between-year differences in the number of calling males in each study plot using a Generalized Linear Model (GLM). We specified the number of calling males in each study plot as the dependent variable and year and plot ID as predictors. We fitted data using a Poisson distribution with a log link function.

To examine whether territories were established in the same locations, we calculated the distance between each male observed in a particular breeding season and the nearest male observed in the previous breeding season. We analyzed four sets of data for the breeding seasons: 2014–2015, 2015–2016, 2016–2017 and 2017–2018. We assumed that the average territory size was equal to an area with a radius of 100 m (less than half the nearest-neighbor distance for the studied population in 2015, when the average nearest-neighbor distance was the lowest—243 m).

To examine whether Corncrake territories were established in locations characterized by different NDVI than average for the study area we compared differences in NDVI in the middle of the breeding season between calling places and the same number of randomly assigned control points (100-m radius around point) using a GLM. We generated the same number of control points as Corncrake territories in each year using the Create Random Points tool in ArcGIS software (Environmental Systems Research Institute, version 10.60). Control points were randomly selected within whole study area (46 km²); thus, the points represented typical vegetation conditions within the study area and could be located in any habitat type inside or outside of the observed territories of calling males. We calculated the NDVI of occupied and control territories as a weighted mean, using the proportion of a pixel within a territory as a weight. In

our model, the dependent variable (calling place vs control point) was fitted using a binary distribution and logit link function. In the model we included two predictors: NDVI and Year. However, the relationship between Corncrake occurrence and habitat conditions described by NDVI may be non-linear. Therefore, we also considered in the models the third predictor—a quadratic term of NDVI (NDVI²). Such an approach enabled us to examine general preferences to NDVI as well as potential differences in preferences of males in years with low and high values of NDVI. We built GLMs with all possible combinations of predictors and their interactions, beginning from the model with one predictor (Year or NDVI) to full model (YEAR + NDVI + NDVI² + YEAR × NDVI + YEAR × NDVI²). Then, we selected the best-fit model using Corrected Akaike Information Criterion (AICC; Burnham and Anderson 2002). For models with Δ AICC of less than nine points (Arnold 2010; Burnham et al. 2011) we calculated Akaike weights (w_i), which can be considered as the probability that a given model is the best approximating model (Symonds and Moussalli 2011). Finally, we interpreted the best-fit model.

To examine whether habitat conditions affect population size, we used a Generalized Linear Mixed Model (GLMM). We specified study plot as a subject variable and year as a within-subject variable. The dependent variable (number of males within a study plot) was fitted by negative binomial distribution and log link function. We included into the model as predictors: one factor (Year) and four covariates and their quadratic terms: (1) NDVI at the beginning of the breeding season, (2) NDVI in the middle of the breeding season, (3) NDVI at the beginning of the previous breeding season, (4) NDVI in the middle of the previous breeding season (an average value of NDVI per study plot). Quadratic terms of NDVI were considered as candidate variables into the models because relationship between NDVI and the Corncrake abundance may be non-linear and may reach some asymptote at high values of NDVI (Heuermann et al. 2011; Zhang et al. 2015). To examine whether linear or linear and quadratic term of NDVI better explain the number of calling male Corncrakes, for each from four types of NDVI, we compared the AICC of two regression models: (1) model comprising only the linear term of NDVI and (2) model comprising the linear plus the quadratic term of NDVI (Riberiro et al. 2019). If the regression model with the quadratic term had a better fit, both the linear and the quadratic terms were included in the GLMM, if not, only linear term was included.

We also analyzed potential multicollinearity between various kinds of NDVI. The highest significant correlation between predictors was observed between the NDVI at the beginning of the breeding season and the NDVI in the middle of the breeding season (Pearson correlation; $r = 0.727$, $p < 0.001$; remaining correlations between predictors

1–3: $r = -0.502$, $p < 0.001$; 1–4: $r = -0.091$, $p = 0.531$; 2–3: $r = -0.246$, $p = 0.08$; 2–4: $r = 0.161$, $p = 0.265$; 3–4: $r = 0.404$, $p < 0.01$). We calculated a variance inflation factor (VIF) for our predictors, which was always lower than 3.0 (the highest VIF was 2.782), meaning that our model did not suffer from multicollinearity and so we can put correlated predictors into one model.

Finally, we built main effects models with all possible combinations of predictors (Year and four types of NDVI). We did not choose a single best-fit model but rather interpreted all models with an ΔAICC of less than nine points (Arnold 2010; Burnham et al. 2011). For these models, we calculated Akaike weights (w_i).

Normality of distribution, when it was necessary, was assessed using a Kolmogorov–Smirnov test. Statistical analyses were performed using IBM SPSS Statistics 24. All p -values are two-tailed.

Results

Changes in male abundance and distribution

We found significant differences in population size between years (GLM: Wald $\chi^2 = 9.71$, $df = 4$, $p = 0.045$) and study plots (GLM: Wald $\chi^2 = 20.319$, $df = 1$, $p = 0.016$). The population of Corncrake ranged from 32 to 58 calling males (Fig. 2). The largest decline was observed between 2014 and 2015 (from 58 to 38 calling males; 34% decrease), while the largest increase was observed between 2017 and 2018 (from 34 to 41 calling males; 21% increase). During a single survey, we recorded between zero and eleven calling males per study plot. The average nearest-neighbor distance ranged from 243 m ($SE = 31.1$) in 2015 to 380 m ($SE = 30.3$) in 2017 (2014 = 249 m, $SE = 14.4$; 2016 = 338 m, $SE = 58.2$; 2018 = 264 m, $SE = 23.3$).

Fig. 2 Observed mean ($\pm$ SE) number of calling male Corncrakes per study plot between 2014 and 2018

To determine whether territories were established in the same places in consecutive years, we assessed a total of 145 territories (38 territories occupied in 2015, 32 in 2016, 34 in 2017 and 41 in 2018). Overall, 46 out of 145 males (32%; $SE = 3.9$) established a territory less than 100 m from the location of calling males in the previous year. The proportion of territories occupied in the same place during two consecutive breeding seasons ranged from 24 to 47% (2015–47%, $SE = 8.2$; 2016–28%, $SE = 8.1$; 2017 – 24%, $SE = 7.4$; 2018–27%, $SE = 7.0$).

Site fidelity of adult males

In total, we caught and individually marked: 2015–56 males, 2016–40 males, 2017–57 males. All males were adults, i.e., birds in the second calendar year or older. The annual return rate of male Corncrakes was very low, with just one out of 56 birds (2%) from 2015 recaptured in 2016 and two out of 40 (5%) from 2016 recaptured in 2017, an overall return rate of 3%. All recaptured males were observed in the same study plot as in the previous year.

For within-season territory fidelity (3–10 days interval between captures, on average 6.3 days), of 47 males caught during the first visit, 17 (36%) were recaptured in the same territory, 12 (26%) were observed calling but did not approach the speaker, three (6%) were new (previously unmarked) males, while no birds were observed in 15 territories (32%).

Habitat conditions and population changes

The best-supported model showed that Corncrake occurrence significantly varied between breeding seasons (Year: $\chi^2 = 10.018$, $df = 1$, $p = 0.040$; Table 1), males occupied territories (100 m radius around calling place) characterized by a significantly higher NDVI (NDVI: $\chi^2 = 17.234$, $df = 1$, $p < 0.001$; Table 1, Fig. 3, S1) than those observed in random points within the study area, and the probability of male occurrence decreased after reaching some asymptote of NDVI (NDVI²: $\chi^2 = 13.488$, $df = 1$, $p < 0.001$; Table 1, S1).

Analysis of candidate variables to the GLMMs examining dependency between Corncrake abundance and habitat conditions showed that regression model with a linear term had lower AICC than regression model with a linear plus quadratic term in the case of NDVI at the beginning of the breeding season, NDVI in the middle of the breeding season, NDVI at the beginning of the previous breeding season; while, the model with a linear and a quadratic term of NDVI in the middle of the previous breeding season had lower AICC than the model with the linear term only (S3). These four variables were considered in the further GLMMs selection process.

Table 1 Results of a GLM of male Corncrake occurrence as a function of habitat conditions (NDVI, NDVI²) and year

Top-ranked models	K	AICC	ΔAICC	w _i	
YEAR + NDVI + NDVI ² + YEAR × NDVI + YEAR × NDVI ²	5	526.527	0	0.409	
YEAR + NDVI + NDVI ² + YEAR × NDVI	4	527.396	0.869	0.265	
YEAR + NDVI + NDVI ² + YEAR × NDVI ²	4	527.963	1.436	0.200	
YEAR + NDVI + NDVI ²	3	529.804	3.277	0.079	
YEAR + NDVI	2	531.432	4.905	0.035	
YEAR + NDVI + YEAR × NDVI	3	533.665	7.138	0.012	
Best-supported model	B	SE	Wald χ^2	df	p
(Intercept)	− 56.637	19.1272	8.768	1	0.003
Year					
2018	35.304	24.9141	2.008	1	0.156
2017	− 8.834	28.9696	0.093	1	0.760
2016	43.751	22.1896	3.888	1	0.049
2015	48.031	21.1716	5.147	1	0.023
NDVI	279.675	99.6427	7.878	1	0.005
NDVI ²	− 339.632	129.3158	6.898	1	0.009
YEAR × NDVI					
2018 × NDVI	− 196.494	128.0012	2.357	1	0.125
2017 × NDVI	97.459	165.0490	0.349	1	0.555
2016 × NDVI	− 225.659	116.9292	3.724	1	0.054
2015 × NDVI	− 236.174	114.8391	4.229	1	0.040
YEAR × NDVI ²					
2018 × NDVI ²	267.130	163.8115	2.659	1	0.103
2017 × NDVI ²	− 192.159	236.3768	0.661	1	0.416
2016 × NDVI ²	289.891	153.5776	3.563	1	0.059
2015 × NDVI ²	288.438	157.5218	3.353	1	0.067

Model was fitted with a binary distribution and logit link function. 2014 and control point were used as a reference for predictor (Year) and dependent variable (territory vs control point). Table shows top-ranked GLMs ($\Delta AICC < 9$) and parameter estimates of the best-supported GLM. *K* the total number of predictors included in the model, *AICC* Corrected Akaike Information Critrion, $\Delta AICC$ differences between the best-supported model and the next models, *w_i* Akaike weights

Fig. 3 Mean (an arithmetic mean $\pm$ SE) values of NDVI within 100 m around calling male Corncrake locations ('territories') and random control points during 2014–2018

Five models received high support (Table 2). In the first three best-supported models (models no. 1–3), there was a significant negative effect of NDVI at the beginning of the previous breeding season. These three models also showed significant differences in the number of calling male Corncrakes between years. Two next models (models no. 4 and 5) show no significant effect of analyzed predictors (Table 2). No model showed significant dependency between NDVI in the current breeding season and Corncrake abundance. The best-supported model (model no. 1; Tables 2, 3) had a w_i of 0.822 which can be interpreted as there being an 82.2% chance that this model is really the best approximating model describing the data from the five considered models. In this model, the number of calling males was significantly negatively correlated with the NDVI measured at the beginning of the breeding season in the previous year and differed significantly between years (Table 3). Data are available in supporting online materials (S2).

Discussion

In our study, we put together a few pieces of the puzzle for Corncrake ecology: (1) significant annual differences in local population size (from 34% decrease to 21% increase), (2) low site fidelity of adult male Corncrakes (2–5% of males returned into the same study plots in a subsequent year), (3) territory shifts both within- and between seasons, (4) strong selection for high values of NDVI (i.e., preference for areas covered by dense vegetation and avoidance of mowed areas characterized by low NDVI values), and

Table 3 Parameter estimates of the best-supported GLMM of male Corncrake abundance

Parameter	B	SE	<i>t</i>	<i>p</i>
(Intercept)	− 8.988	8.651	− 1.039	0.305
Year				
2014	− 1.484	0.545	− 2.721	0.010
2015	− 0.870	0.562	− 1.549	0.129
2016	− 1.291	0.430	− 3.005	0.005
2017	− 0.904	0.622	− 1.454	0.154
NDVI beginning	− 0.948	3.766	− 0.252	0.802
NDVI middle	1.855	4.481	0.414	0.681
NDVI beginning in previous year	− 9280	3.430	− 2.706	0.010
NDVI middle in previous year	41.304	36.324	1.137	0.262
NDVI ² middle in previous year	− 24.803	36.669	− 0.676	0.503

(5) a strong negative effect of NDVI in the previous breeding season on population size. Taking all into consideration, we hypothesize that male Corncrakes may utilize nomadic breeding behavior as a response to changing habitat conditions (onset of vegetation growth and extent of flooding and mowing). We observed low annual site fidelity of adult males at a territory scale, even when assuming extremely high mortality of adult males (0.7–0.8) (Green 2004); as well as within-seasonal territory shifts. The nomadic breeding hypothesis for the Corncrake is also supported by the long-distance movements of males recorded within a breeding season (Koffijberg et al. 2016). Furthermore, Mikkelsen et al. (2013) observed that in Norway, male Corncrakes

Table 2 Top-ranked GLMMs ($\Delta AICC < 9$), predicting the abundance of male Corncrakes

Model no	Model	K	AICC	$\Delta AICC$	w_i
1	Year [*]+NDVI B [↔]+NDVI M [↔]+ NDVI BPY [↓*]+NDVI MPY [↔]+NDVI MPY ² [↔]	6	55.459	0	0.822
2	Year [*]+NDVI M [↔]+ NDVI BPY [↓*]+NDVI MPY [↔]+NDVI MPY ² [↔]	5	59.000	4.541	0.140
3	Year [**]+ NDVI BPY [↓**]+NDVI MPY [↔]+NDVI MPY ² [↔]	4	63.657	8.198	0.014
4	NDVI B [↔]+NDVI M [↔]+NDVI BPY [↔]+NDVI MPY [↔]+NDVI MPY ² [↔]	5	63.863	8.404	0.012
5	Year [↔]+NDVI B [↔]+NDVI M [↔]+NDVI MPY [↔]+NDVI MPY ² [↔]	5	63.974	8.515	0.012

Models were fitted with a negative binomial distribution and log link function. Table includes: the total number of predictors included in the model [K], Corrected Akaike Information Criterion (AICC), differences between the best-supported model and the next models [$\Delta AICC$], Akaike weights [w_i]. Negative [↓], positive [↑] or neutral [↔] relationship among predictor and number of Corncrake males is shown

Predictors codes indicate: *Year* year of survey, *NDVI B* NDVI at the beginning of the breeding season, *NDVI M* NDVI in the middle of the breeding season, *NDVI BPY* NDVI at the beginning of the previous breeding season, *NDVI MPY* NDVI in the middle of the previous breeding season, *NDVI MPY²* quadratic term of NDVI in the middle of the previous breeding season. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

actively looked for the best territories and frequently moved long distances during the breeding season. Such a breeding strategy is observed in many polygynous species in which males only compete for access to fertile females and do not invest in care for the offspring (Emlen and Oring 1977). Thus, males move through a considerable part of the entire species breeding range and visit multiple breeding areas to increase their chances of reproduction (Kempnaers and Valcu 2017). For Corncrakes, within-season movements on a continental scale are mainly enforced by mowing activity, after which suitable breeding habitat is lost for many weeks. The nomadic behavior hypothesis is also supported by weak geographic variation in call characteristics among populations, which is probably the result of a common movement of males between populations (Budka et al. 2014). Moreover, existing high genetic diversity in European populations but with no geographic pattern suggests strong gene flow between populations (Fourcade et al. 2016). We also found that only 24–47% of the territories were located in approximately the same locations as those established in the previous year. In some species, such a degree of site fidelity could be explained by high levels of natal philopatry (Camacho 2014) or adult breeding site fidelity (Sedgwick 2004). In the case of the Corncrake, however, both hypotheses are unlikely. The results from this study showed that adult males rarely return to the same territories or even location in the following season. The true level of site fidelity, however, may be higher than that recorded here since males may show a weaker response to playback with repeated use, as suggested by the low recapture rate of those present on second visits. Therefore, low territory fidelity may be explained by a seasonally variable spatial distribution of optimal habitat patches. Regardless of whether or not individuals come from a local population, they should occupy patches of optimal habitat first and, thus, maximize their fitness (Betts et al. 2008). Some variation in the spatial distribution of males among years could be explained by seasonal variation in habitat management (e.g., not managing certain fields, changes in mowing pattern), local microhabitat changes or individual variation in habitat preferences.

Following the nomadic breeding behaviour hypothesis, we expected that male Corncrakes should establish territories in a particular location only when habitat conditions in the spring are optimal (e.g., presence of dense, tall vegetation); otherwise, they may fly many kilometers further away. In our model, the NDVI at the beginning as well as in the middle of the breeding season had no effect on population size. The specific nature of our location was that meadows were managed extensively in ca 60% of the area and thus, after arriving from wintering grounds, males would have met many patches of tall vegetation from the previous year, which is strongly preferred by Corncrakes (Budka and Osiejuk 2013). Instead, the significant predictor of population

size was the NDVI at the beginning of the previous breeding season, meaning that the most important factor is not what is going on now but what occurred in the previous year. Suitable vegetation in the course of the season enhances the chances for Corncrakes to breed successfully (Wotton et al. 2015; Bellebaum et al. 2016). Hence, higher reproductive output may result in more Corncrakes returning to the area one year afterwards. The survival rate and dispersal pattern of chicks are similar to that of adults, but with a tendency to undertake even longer movements (Green 1999). Thus, we suppose that local population changes may reflect a more general trend in a whole population rather than local breeding success, since even high breeding success in previous years would not be able to cause the observed population growth without immigration of birds from outside the local population. In summary, we suggest that suitable weather conditions determine optimal vegetation growth and mowing activity on a regional scale leading to higher reproductive success and, as a consequence, more second-year birds are recruited into the population in the following year. Our best-supported model showed the potential threat of good habitat conditions at the beginning of the previous year. In this model, population size was negatively correlated with NDVI at the beginning of the previous breeding season (Table 3). This can be explained by more frequent settlement of Corncrakes in intensively managed meadows during years with fast-growing vegetation for which mortality rates of broods due to mowing are much higher (Tyler et al. 1998). After such negative experiences related to brood losing, females may show a tendency to return into extensively management habitats in the next year, like those in our study area. In such scenarios, effective management and conservation of Corncrakes should be undertaken at the population level. This then raises the question, at what level of conservation coordination (regional, national or international) is sufficient for population maintenance? Local Corncrake-friendly management schemes play a very important role in increasing female and chicks survival (Tyler et al. 1998), but may be insufficient to conserve the species population on a global scale. For example, high breeding success observed in a local protected population may not be sufficient to keep that population stable especially when birds do not return to the natal location, but exhibit a nomadic breeding behaviour. This may also occur when high mortality occurs outside the breeding area. This mechanism was described clearly by Bellebaum and Koffijberg (2018). They showed that agri-environment measures are effective when covering a considerable portion of the breeding population, but do not positively affect Corncrake population trends when only a small portion is covered, as seen in eastern Europe. We, therefore, highlight the need for a better understanding of dispersal patterns of Corncrake populations in mainland Europe and the coordinated deployment of monitoring and

conservation activities on an international scale, especially in those regions where most Corncrakes breed.

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