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Corncrake conservation genetics at a European scale: The impact of biogeographical and anthropological processes



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ABSTRACT

Understanding patterns of genetic structure, gene flow and diversity across a species range is required to determine the genetic status and viability of small peripheral populations. This is especially crucial in species distributed across a large range where spatial heterogeneity makes it difficult to predict the distribution of genetic diversity. Although biogeographical models provide expectations of how spatially structured genetic variation may be at the range scale, human disturbance may cause strong deviations from these theoretical predictions. In this study, we investigated genetic structure and demography at a pan-European scale in the corncrake Crex crex, a grassland bird species strongly affected by agricultural changes. We assessed population structure and genetic diversity, as well as demographic trends and direction of gene flow, in and among 15 contemporary populations of this species. Analyses revealed low genetic structure across the entire range with high levels of genetic diversity in all sites. However, we found some evidence that the westernmost populations were, to a very limited extent, differentiated from the rest of the European population. Demographic trends showed that population numbers have decreased in western Europe and remained constant across eastern Europe. Results may also indicate asymmetric gene flow from eastern to western populations. In conclusion, we suggest that the most likely scenario is that contrasting demographic regimes between eastern and western populations, driven by heterogeneous human activity, has caused not only asymmetric gene flow that has buffered small peripheral populations against genetic diversity loss, but also erased any genetic structure that may have existed. Our study not only highlights the need for coordinated action at the European scale to preserve source populations of the corncrake, but also to ensure persistence of the most threatened sites. Only by doing so will we avoid losing adaptive potential and prevent over-reliance on eastern source populations whose future may be uncertain.

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1. Introduction

Spatial heterogeneity in the environment is an important factor affecting widely distributed species (Pickett and Cadenasso, 1995). The distribution of factors such as ecogeographic regions, natural barriers to dispersion, migration routes, or other organisms such as competitors,

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predators or pathogens, may vary over spatial scales and affect overall connectivity and local adaptation in any focal species. Similarly, when a species' range overlaps several countries, it may be affected by the ecological impact of different levels of economic development and environmental awareness (Dallimer and Strange, 2015). Therefore, the distribution of genetic variation across a species' range often emerges from a complex interaction between natural biogeographic and anthropogenic processes. However the pattern of the biological component (Moilanen and Arponen, 2011). If the relative contribution of the latter is strong enough it may be difficult to use classical biogeographical models to predict the range dynamics of a focal species, and thus to make and implement international conservation plans. Ad-hoc models

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of range dynamics may need to be developed for such species. Information on gene flow and demographic trends across a range are key to identifying Evolutionarily Significant Units (ESU, Ryder, 1986) and evaluating the threats associated with changes in connectivity, i.e. inbreeding depression or the loss of adaptive potential (Hedrick and Kalinowski, 2000). Therefore such knowledge is critical in the design of informed conservation action plans.

Biogeographic models of range dynamics provide predictions regarding patterns of genetic variation across a species' distribution. Under the central-marginal model, focal species abundance is expected to be higher at the range core (i.e. the area of ecological optimum), and less abundant and more isolated at the periphery as environmental conditions gradually depart from the ecological optimum (Hengeveld and Haeck, 1982; Brussard, 1984; Brown, 1984). This has implications for the distribution of genetic variation at the range-scale (Eckert et al., 2008) and for the evolution of species' range (Hoffmann and Blows, 1994; Kirkpatrick and Barton, 1997). Although the central-marginal model is widely accepted, the hypothesis has been challenged by empirical and theoretical studies (Sagarin and Gaines, 2002; Sagarin et al., 2006; Samis and Eckert, 2007) and the model itself can generate opposite patterns. A first hypothesis implies that populations at the core have higher effective population sizes and produce more dispersing migrants than do the smaller, peripheral populations. Under this model, genetic drift in the peripheral populations is only partially compensated by limited gene flow from the core area, and therefore results in lower genetic diversity in, and higher differentiation among, these peripheral populations (Hoffmann and Blows, 1994; Lesica and Allendorf, 1995; Eckert et al., 2008). Consequently, these marginal populations are expected to be more sensitive to environmental changes - either stochastic or directional - and more prone to extinction (Lesica and Allendorf, 1995; Channell and Lomolino, 2000). In contrast, a second hypothesis suggests that if core populations are large and peripheral populations are small, there could be asymmetric gene flow from core to periphery (Kirkpatrick and Barton, 1997) analogous to that expected in a source-sink (Pulliam, 1988), or island-continent model (Slatkin, 1987). Homogenisation of genetic diversity and weak structure at the range scale is expected if the effect of the asymmetric gene flow is greater than the combined effects of drift and selection at the range margins.

Importantly, human disturbance, by disrupting natural dynamics, may counteract the theoretical assumptions outlined above. Indeed, anthropic activity can result in barriers to gene flow, fragmenting species ranges and increasing genetic isolation between populations (Keller and Largiader, 2003). On the contrary, human-assisted dispersal, or the creation of corridors through changes of landscape structure, can favour genetic mixing between previously isolated populations (Hale et al., 2001). Human activity frequently affects the growth of wild populations, either positively (Garrott et al., 1993), or negatively (Butchart et al., 2010), altering natural demographic trends and thus influencing the genetic characteristics of these populations. Moreover, climate change, by driving a rapid shift in species distributions, may further blur previously existing biogeographical patterns. Therefore, a combination of natural and anthropogenic dynamics is responsible for the observed patterns of genetic variation at large-scale. Thus it is important to consider both processes in interpreting the levels of population differentiation, or differences in genetic diversity, that are observed across the range of a species.

We used the corncrake (*Crex crex*) as a model species to study genetic structure and gene flow at a continental scale. As is the case for many grassland bird species (Donald et al., 2006), agriculture intensification has severely affected the number and distribution of the corncrake (Green et al., 1997). This situation has motivated numerous conservation plans, especially in western Europe. Interestingly, because land use change and agriculture intensification are variable across Europe, the corncrake has been affected by human activity at various intensities in different parts of its range. To date, knowledge regarding genetic structure in this species is very limited and incomplete (Wettstein, 2003) and other methods (e.g. monitoring returning individuals) do not provide adequate amounts of data to determine dispersal patterns, connectivity between sites, or identify distinct evolutionary significant units in this species (Ryder, 1986). Interestingly the extensive population monitoring of the corncrake undertaken in many European countries allows survey-based demographic trends to be compared against the historical demography inferred using genetic data. The availability of such fine-scale demographic data provides an exciting opportunity to determine if apparent local trends, which usually drive conservation actions, concur with the continental-scale demographic landscape. Specifically, we tested two competing hypotheses arising from the centralmarginal model: 1) peripheral populations are isolated from the core populations and are thus genetically differentiated and show a reduction of genetic diversity, 2) demographic imbalance between core and peripheral populations generates net gene flow towards the periphery that homogenises populations across the range. We used a suite of microsatellite markers to assess genetic diversity and structure across the European range of the corncrake. Approximate Bayesian computation (ABC) (Beaumont et al., 2002) was used to estimate corncrake historical demography at the population scale in order to assess fine-scale spatial variation in demographic trends across Europe. In order to assess the dynamics generating the observed pattern of genetic structuring, an ABC framework was also used to determine the direction of gene flow between western and eastern populations.

2. Methods

2.1. Study species and sample collection

The corncrake is a migratory bird that breeds on grasslands across the Palearctic (Schäffer and Koffijberg, 2004). Ecological niche modelling (Fourcade et al., 2013) and expert field knowledge (Schäffer and Koffijberg, 2004) suggest that the species' range core is located in Russia and eastern Europe, while favourable habitats are scarcer and more fragmented in western Europe. Changes in anthropogenic activities, e.g. the intensification of agricultural practices, have contributed to creating large demographic differences across the species range. In western Europe, numbers have declined severely (Green and Gibbons, 2000; Deceuninck et al., 2011) but the situation in eastern Europe/ Asia, which includes 90% of the world's corncrake population (Schäffer and Koffijberg, 2004) is fundamentally different. In the east the impact of agriculture intensification during the 20th century is difficult to assess, but was probably less important than in western Europe. Indeed recent surveys highlight the positive effect of agricultural abandonment after the demise of the USSR on corncrake populations (Keišs, 2005; Mischenko, 2008). Although dispersal patterns are unclear in this species due to a very low recovery rate of ringed birds (<5%, Green, 1999), there is some evidence of long-distance movement (>500 km) within the breeding season (Schäffer and Koffijberg, 2004; Mikkelsen et al., 2013). We focus on the European part of the corncrake's range. This includes a core area (eastern Europe) in which corncrakes are relatively abundant and evenly distributed, surrounded by several smaller populations in the north (Sweden), west (Scotland, France) and south (Romania, Italy) of the range.

With the collaboration of local ringers we collected 496 corncrake samples from 15 locations across Europe (Fig. 1) in 2011–2012. Samples were collected from May to July to avoid the capture of migrating birds. Individuals were attracted using playback of conspecific male calls at night during the peak of calling activity and captured using a mist net or large dipnet. Because of the playback-assisted capture method only males were sampled (Green, 1999). Depending on the local legislation and experience of the fieldworkers, different sources of DNA were collected. The different tissues sampled did not affect the quality of DNA extracted or the accuracy of the genotyping. In France, Germany, Italy, Hungary, Poland (all sites), Czech Republic, Latvia, Belarus and Russia (20 samples out of 32), ca. 50 µL of blood was collected from the brachial

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