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How weather conditions in non-breeding and breeding grounds affect the phenology and breeding abilities of white storks

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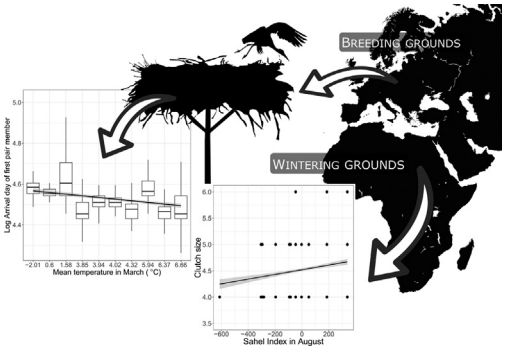
HIGHLIGHTS

- The relationship between rainfall, temperature and ecology of white stork is presented.
- Long-term data on white stork breeding were used to test the carry-over effect.
- Egg size and number were dependent on conditions in the wintering grounds.
- Birds breeding abilities are dependent on both breeding and non-breeding period.
- Breeding success is dependent on weather conditions on the breeding grounds.

GRAPHICAL ABSTRACT



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ABSTRACT

Background: It has often been suggested that conditions in wintering grounds affect the breeding abilities of migratory birds. This is known as the *carry-over effect*. Heretofore, many studies have reported the relationship between conditions in wintering grounds, dates of departure from and arrival at breeding grounds, and breeding success. However, very few studies have shown how these conditions affect the capacity of females for egg production.

Aims: To describe how conditions in the remote non-breeding areas in Africa affect reproductory abilities of migratory birds breeding in Europe.

Methods: We recorded 863 arrival dates for 191 nests (in 2005–16), clutch sizes of 412 clutches, and egg dimensions of 1725 eggs (in 2003–16) of white storks in western Poland. We used generalised climatic indicators such as the Sahel precipitation index (SPI) and Indian Ocean Dipole (IOD) to assess conditions in wintering grounds prior to breeding and precipitation and temperature in breeding grounds during the breeding season.

Results: The white stork arrived significantly earlier in seasons preceded by a warmer and rainier March, while conditions in Africa did not affect arrival dates. Females laid more (and larger) eggs in seasons preceded by rainier winters in Africa. Breeding success was not affected by conditions in wintering grounds, but only by the weather during breeding season.

Conclusions: Conditions in wintering grounds may affect migratory birds, not only in terms of their arrival dates, but rather with respect to females' egg production capacities. Studies on stable isotopes may yield more detailed findings as to how this process takes place.

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1. Introduction

One of the most important drivers of animal population dynamics is reproductive success (Pulliam, 1988). In bird populations, this is strongly influenced by current environmental variables in breeding grounds, such as weather conditions (Moreno and Møller, 2011; Rodríguez and Bustamante, 2003), food resources (Hoy et al., 2016), and inter- and intraspecific competition (Newton, 2008). In studies on sedentary organisms, identifying the most important predictors of population productivity is not a difficult matter. However, incorporating seasonality of occupied habitats into analyses is necessary for understanding biology of species (Waite and Strickland, 2006; Whelan et al., 2016). In the study of migratory animals environmental variables, in both breeding and, in particular, non-breeding areas visited by the studied species, must be accounted for (Norris, 2005). Nevertheless, both migratory and sedentary species face extremely different weather and environmental conditions during the annual cycle, which may have consequences for breeding. In the case of migratory birds whose life cycle involves spending the majority of each year outside their breeding grounds, it is difficult to identify the environmental components which drive their fitness. Moreover, it is sometimes impossible to do so without the application of techniques such as geolocators or transmitters (e.g. Bächler et al., 2010; Thorup et al., 2017; Van Den Bossche et al., 2002). Fortunately, for large-bodied bird species, migratory paths and year-round cycles are well studied and for many species we are able to extrapolate where birds are during particular time in the annual cycle.

Climate is one of the most important factors driving bird migration. Weather conditions may affect migratory birds through reducing survival rates in both breeding (Moreno and Møller, 2011, Robinson et al., 2007) and wintering grounds (Peach et al., 1991; Sicurella et al., 2016; Szép, 1995; Schaub et al., 2005). Conditions in wintering grounds do not affect the survival of juvenile/immature and adult/breeders of a given species equally. Conditions in Africa may reduce the survival of juveniles more drastically than that of adults. This is probably due to the greater experience of adults in foraging in wintering grounds (Schaub et al., 2005). Moreover, when the impact of weather is not lethal, it may manifest as a change in the timing of migration (Both and te Marvelde, 2007; Charmantier and Gienapp, 2014; Hüppop and Winkel, 2006; Rainio et al., 2006), arrival at the breeding grounds (Gordo et al., 2005; Kaňuščák et al., 2004; Macmynowski et al., 2007; Saino et al., 2004; Studds and Marra, 2011; Tryjanowski et al., 2002; 2005), or the breeding process itself (Both and te Marvelde, 2007; Charmantier and Gienapp, 2014; Visser et al., 2009). Nevertheless, the survival costs paid by migratory birds for survival in non-breeding grounds should be reflected during the subsequent breeding season in reproductive success value. Also for sedentary birds, costs of survival in breeding territory year round may be costly and have negative consequences in reproduction (Waite and Strickland, 2006; Whelan et al., 2016). This is known as the *carry-over effect* (Norris et al., 2004; Norris, 2005), and it occurs especially in long-lived species which can allocate their breeding investment over several breeding seasons as an effect of experience gained from previous breeding attempts (Senner et al., 2015). The breeding success of migratory birds is an effect of arrival at the breeding grounds, clutch size, and nestling survival rate. Arrival at the breeding grounds is, in turn, an effect of the current quality of individuals. In theory, the best breeders arrive first and occupy the best territories (Kokko, 1999). However, there are several costs of very early arrival, i.e. exposure to very severe weather conditions and, in consequences, a lower breeding success (Janiszewski et al., 2013; Vergara et al., 2007; Tryjanowski et al., 2004). Hence, birds tend to arrive in optimal time, in terms of weather and food resources. Arrival dates are driven by weather and food conditions in the wintering grounds. Rainfall and food resources in staging areas affect departure times, i.e. in drier winters, individuals depart significantly later than in wet winters, which has an effect on arrival dates (Saino et al., 2004; Studds and Marra, 2011). Assuming that wintering grounds differ in quality, the particular habitat patch where birds spend the winter may also affect the date breeding is initiated (Schamber et al., 2012), which is correlated with arrival. However, this may be modified by weather conditions during the last part of the return passage (Gordo et al., 2013; Shamoun-Baranes et al., 2003), or even by weather in the breeding grounds which is correlated with weather conditions on the last part of spring migration (Ptaszyk et al., 2003; Tobolka et al., 2015).

The second component of breeding success is egg production (clutch size) - laying capacity. It is still not certain where females accumulate the resources for producing eggs. However, in the case of the white stork *Ciconia ciconia* (Hungarian population), clutch size was negatively correlated with the number of cold days in the breeding grounds prior to egg laying (Sasvári and Hegyi, 2001). Nevertheless, for the Polish white stork population, no relationship has been shown between weather in the breeding grounds prior to egg-laying and clutch size (Tobolka et al., 2015), which does not support the hypothesis that females collect egg substrates from breeding grounds and therefore, the number of eggs is primarily dependent on conditions in other areas. These findings suggest that weather may regulate the current quality of females, which is established before the breeding season. However, it is not only the number of eggs laid that affects final breeding output. Egg dimensions, which are an effect of female quality (Slagsvold and Lifjeld, 1990; Wendeln, 1997), can strongly affect hatchlings' body size (Amundsen and Stokland, 1990) and hence their survival, as well as the number of fledglings and their fitness (Blomqvist et al., 1997; Williams, 1994). However, final breeding success seems to be rather independent of conditions in non-breeding areas prior to breeding season. In altricial birds it is mostly dependent on weather conditions during the rearing of nestlings and on food abundance (Hoy et al., 2016; Moreno and Møller, 2011; Tobolka et al., 2015).

In this paper we examine the influence of weather conditions in wintering and breeding grounds on the breeding biology of a long-lived bird species, namely, the white stork, which is an example of a long-distance trans-African migratory bird. Based on both ringing recoveries and satellite tracking data, we know that the Eastern migratory white stork subpopulation studied in this paper spends the winter in the Sahel area (October and November) and extends its migration to central-eastern and southern Africa (November–February) (Kania, 1985, 2006; Van Den Bossche et al., 2002). The population starts back in February and arrives at the breeding grounds in Europe in early spring (March and April). The arrival dates are strongly influenced by the weather prior to and during arrival (Ptaszyk et al., 2003; Shamoun-Baranes et al., 2003; Tobolka et al., 2015). Usually pair members arrive to their territories separately, males firstly and females several days later (Gordo et al., 2013) but arrivals of both partners are strongly correlated. After on average 12 days (range: 1–30), females lay an egg (Tryjanowski et al., 2004). The birds build open nests atop man-made structures such as poles, roofs of buildings, and chimneys, as well as, rarely, on trees (Tobolka et al., 2013). The female lays 1–6 eggs, which are incubated for ca 30 days. Fledglings leave the nest after ca 55 days. Brood survival is strongly dependent on weather conditions in the breeding grounds (Tobolka et al., 2015).

Using data on arrivals, along with several breeding parameters, we test here the following hypotheses. (1) The weather on the wintering and breeding grounds influence bird's arrival on the breeding sites. (2) The number of laid eggs and their dimensions are affected by rainfall (and therefore food abundance) in the winter staging areas in the Sahel. (3) Breeding success is affected by weather conditions in both the breeding and wintering grounds.

2. Material and methods

2.1. Data collection

The study was conducted in western Poland near the town of Leszno (51°51′ N, 16°35′ E) in an area of agricultural landscape measuring