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Wintering in Europe instead of Africa enhances juvenile survival in a long-distance migrant

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Increased human-induced environmental changes and global warming alter bird migration timing and routes. Recently, many Holarctic species, including white storks, *Ciconia ciconia*, were reported to overwinter at higher latitudes, closer to breeding grounds. We aimed to understand the causes and implications of this phenomenon by examining bird survival and behaviour during overwintering in Europe versus Africa. We compared GPS and body acceleration data of 54 juvenile (first-year) white storks that originated from the same European natal population and overwintered in Europe or Africa. All six juveniles that overwintered in Europe survived through their first year, which was significantly higher than only 38% of the 48 overwintering in the species' traditional grounds in Africa. During overwintering, storks in Europe differed from those in Africa by (1) reducing movement and foraging range, (2) spending less time flying and more time resting, thus using less energy (estimated from overall dynamic body acceleration) and (3) reducing foraging effort, while relying more on anthropogenic resources (landfills and agricultural areas). Timing affected overwintering site as juveniles that overwintered in Europe hatched and started migrating later. We emphasize, however, that late hatching by itself did not yield a survival benefit as not all late juveniles curtailed their migration. We suggest that wintering in Europe was less demanding compared to Africa which may explain the increased survival of juveniles that wintered in Europe. Our findings correspond to the general increase in the European wintering population of white storks, and shed light on the contemporary trend of shortened bird migration; a phenomenon with potentially broad ecological implications.

Bird migration provides access to seasonally abundant food resources while avoiding harsh winter conditions (Alerstam, Hedenström, & Åkesson, 2003; Somveille, Rodrigues, & Manica, 2015). However, environmental conditions are changing considerably as human-related food resources increase (Oro, Genovart, Tavecchia, Fowler, & Martínez-Abraín, 2013) and the global climate is warming (IPCC, 2014). Plasticity of bird migration (Able & Belthoff, 1998; Alerstam et al., 2003; Berthold, 1998) allows species to respond to these changes by altering migration timing and routes (Charmantier & Gienapp, 2014; Newton, 2008). In many Holarctic bird species, migration phenology is adjusting towards an earlier arrival to breeding grounds to accommodate the earlier onset of spring (Both, Bouwhuis, Lessells, & Visser, 2006; Hüppop &

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Hüppop, 2003; Marra, Francis, Mulvihill, & Moore, 2005; Newton, 2008).

In recent years, an increasing number of studies have also reported that Holarctic migrants are shortening their migration and overwinter at higher latitudes closer to their breeding grounds (28 species reviewed in Ambrosini et al., 2016; Newton, 2008; Pavón-Jordán et al., 2015; Plummer, Siriwardena, Conway, Risely, & Toms, 2015; Visser, Perdeck, van Balen, & Both, 2009). Some overwinter in sites where they were not previously recorded and, for others, an increased proportion of the population winters at higher latitudes (Newton, 2008; Ramo et al., 2015). Accordingly, in several European migrants that overwinter both in Africa and in Europe, the European overwintering populations are growing (Gordo, Sanz, & Lobo, 2007; Lok, Overdijk, Tinbergen, & Piersma, 2011), probably due to anthropogenic (e.g. landfills and agriculture) food exploitation (Oro et al., 2013; Plummer et al., 2015; Ramos, Ramírez, Sanpera, Jover, & Ruiz, 2009; Sanz-Aguilar, Jovani, Melián, Pradel, & Tella, 2015; Tortosa, Caballero, & Reyes-López, 2002) and the effects of milder winters that increase bird survival (Adriaensen & Dhondt, 1990; Ambrosini et al., 2016; Duriez, Ens, Choquet, Pradel, & Klaassen, 2012; Salewski, Hochachka, & Fiedler, 2013). Conditions at wintering sites have a significant impact on birds' annual survival (Schaub, Kania, & Köppen, 2005; Szostek & Becker, 2015) with major consequences for population dynamics (Alves et al., 2013; Goodenough, Elliot, & Hart, 2009; Ockendon, Hewson, Johnston, & Atkinson, 2012; Schaub et al., 2005) and may trigger changes in migration patterns (Cooper, Sherry, & Marra, 2015; McKellar, Marra, Hannon, Studds, & Ratcliffe, 2013). It is therefore important to study the causes and implications of changes in overwintering patterns.

Recent intriguing findings suggest that birds that shorten their migration to overwinter closer to natal grounds in Europe attain higher survival than conspecifics wintering in traditional overwintering grounds in Africa (Lok et al., 2011; Sanz-Aguilar, Béchet, Germain, Johnson, & Pradel, 2012, Sanz-Aguilar, De Pablo, & Donázar, 2015). However, the underlying mechanisms could not be assessed from these studies which relied on 'mark–resight' methodology. Behavioural data linking recent changes in environmental conditions and bird overwintering shifts are lacking. Here, we aimed to address this gap by comparing GPS and body acceleration (ACC) data of juvenile (first-year) white storks, *Ciconia ciconia*, that overwintered in Europe and Africa.

We studied a stork population that mostly migrates from Europe to Africa (Berthold et al., 2001) along the eastern migratory flyway, via the Middle East, unlike western flyway migrants reported in the studies mentioned above. Storks are opportunistic predators (Bocheński & Jerzak, 2006; Tsachalidis & Goutner, 2002) and, recently, an increasing number of individuals have shortened their migrations to overwinter in southern Europe, particularly in Spain (Gordo et al., 2007; Martín, Onrubia, de la Cruz, & Ferrer, 2016; Shephard, Rycken, Almalik, Struyf, & Van Erp-van der Kooij, 2015; Tortosa et al., 2002) where they utilize landfills and an invasive crayfish *Procambarus clarkii* in rice fields (Aguirre & Vergara, 2007; Peris, 2003; Sanz-Aguilar, Jovani, et al., 2015). To increase our understanding of this contemporary change, we examined differences in survival and behaviour between juvenile storks originating from the same natal region in Germany that overwintered in Europe and Africa. We devised two opposing hypotheses. (1) Survival of African wintering storks should be higher in accordance with the fact that most of the stork population migrate to Africa, where environmental conditions during the northern hemisphere winter are likely to be more suitable. In contrast, (2) the recent increase in the proportion of storks wintering in Europe (Gordo et al., 2007) implies a survival benefit, as has been evident in other migrating species (Lok et al., 2011; Sanz-Aguilar et al., 2012), possibly because of access to sufficient anthropogenic food resources (e.g. landfills) in Europe along with lower costs (flight) and risks (predation, hunting) than when wintering in Africa. We used advanced GPS-body acceleration (ACC) transmitters to compare survival, movement patterns, behaviour, activity-related energy expenditure (derived from overall dynamic body acceleration, ODBA; Wilson et al., 2006) and habitat use during overwintering in Europe versus Africa, aiming to elucidate possible fitness-related differences. We further examined why certain juveniles overwintered in Europe while others overwintered in Africa, testing the hypothesis that late-hatching juveniles, being less fit for the migration (Brown, Roche, & O'Brien, 2015; McKim-Louder, Hoover, Benson, & Schelsky, 2013; Mitchell, Guglielmo, Wheelwright, Freeman-Gallant, & Norris, 2011), were more likely to shorten their journeys and overwinter in Europe.

METHODS

We tagged 92 juvenile storks. For this paper, we analysed data from 54 individuals that reached the wintering period, i.e. survived beyond October (a month after the end of last migratory journey to Africa); more details on the excluded individuals are given in Appendix 1. Juveniles were fitted with solar-charged GPS transmitters (48 from e-obs GmbH, Munich, Germany, weight 54 g, and six from Microwave Telemetry, Inc., Columbia, MD, U.S.A., weight 43 g). Juveniles were trapped in their nests approximately a week prior to fledging, and tagging took place from 2011 to 2014 in the state of Saxony-Anhalt, Germany around three sites: Beuster (52.939°N, 11.787°E), Loburg (52.118°N, 12.087°E) and the Drömling Nature Park (52.489°N, 11.022°E). The transmitter plus harness (12 g) weighed a maximum of 66 g, corresponding to 2% of the mean white stork body mass (Bruderer, Peter, Boldt, & Liechti, 2010).

The transmitters yielded two types of data sets: (1) low-resolution GPS data of 2–10 GPS fixes per day, transmitted remotely via cellular (e-obs tags) or satellite (Microwave tags) communication (see Appendix 2 for details); (2) high-resolution GPS and ACC data recorded every 5 min (e-obs tags only; when solar power was sufficient) from 0200 to 2000 GMT. The ACC was recorded for 3.8 s at 10.54 Hz for each of the three perpendicular axes, totalling 120 data points per ACC sample. The high-resolution data were stored on board the transmitters and were downloaded manually via radio link from approximately 300 m away (see Appendix 2); this was not feasible for all individuals.

Comparison of survival rates between storks wintering in Europe ($N = 6$) and Africa ($N = 48$) was based on the low-resolution GPS data. To compare fine-scale overwintering movement and behaviour, we examined the GPS-ACC high-resolution data from October to December of juveniles overwintering in Europe ($N = 6$) and Africa ($N = 16$) that survived throughout this period. We focused on this period because (1) all tracked individuals reached their overwintering grounds by October and (2) our transmitters depended on solar recharge, so low solar conditions resulted in highly fragmented data in January–February in Europe. Accordingly, solar conditions and sampling rates were higher in Africa than Europe. To eliminate this bias, we subsampled the data of the African wintering (AFW) juveniles in line with the European wintering (EUW) juveniles' data (see Appendix 3 for details). This resulted in a total of 347 392 GPS-ACC records from 1760 wintering days of six EUW juveniles and 16 AFW juveniles. Because white storks are diurnal, and daylight time was shorter for individuals overwintering in Europe, in relevant analyses we examined daylight data (from half an hour before sunrise to half an hour after sunset) that was extracted using the Matlab 'suncycle' function