Modelling migration dynamics of Common Cranes and Eurasian Spoonbills as hydrological flow

Drever, Mark C.; Bautista-Sopelana, Luis M.; Alonso, Juan C.; Navedo, Juan G.; Hrachowitz, Markus

DOI
10.1111/ibi.13424

Publication date
2025

Document Version
Final published version

Published in
Ibis

Citation (APA)
Drever, M. C., Bautista-Sopelana, L. M., Alonso, J. C., Navedo, J. G., & Hrachowitz, M. (2025). Modelling migration dynamics of Common Cranes and Eurasian Spoonbills as hydrological flow. *Ibis*, *167*(4), 962-978. https://doi.org/10.1111/ibi.13424

IBIS
BOU international journal of avian science
Ibis (2025) doi: 10.1111/ibi.13424

Modelling migration dynamics of Common Cranes and Eurasian Spoonbills as hydrological flow

MARK C. DREVER,*[1] LUIS M. BAUTISTA-SOPELANA,[2] JUAN C. ALONSO,[2] JUAN G. NAVEDO[3,4] & MARKUS HRACHOWITZ[5]

[1]*Environment and Climate Change Canada, Pacific Wildlife Research Centre, 5421 Robertson Road, Delta, V4K 3N2, BC, Canada*

[2]*Department of Evolutionary Ecology, National Museum of Natural Sciences MNCN, Spanish Research Council CSIC, José Gutiérrez Abascal 2, Madrid, 28006, Spain*

[3]*Bird Ecology Lab, Instituto de Ciencias Marinas y Limnológicas, Universidad Austral de Chile, Valdivia, Chile*

[4]*Ecology in the Anthropocene, Área de Zoología, Universidad de Extremadura, Badajoz, Spain*

[5]*Department of Water Management, Faculty of Civil Engineering and Geosciences, Delft University of Technology, Stevinweg 1, Delft, 2600 GA, The Netherlands*

The migration of birds through a stopover site may be understood as a physical process of hydrological flow through a reservoir whose water levels rise and fall over a migration period. Hydrological flow models show promise as a way of integrating information on storage (daily counts of birds), inflow/outflow (number of birds arriving/departing each day) and transit time (length of stay (LOS)) over a migration period. We used a hydrological flow model to evaluate the relationship between stopover duration and passage population sizes of migrant birds under variable wetland conditions in two case studies. First, we considered the northward migration of Common Cranes *Grus grus* at Gallocanta Nature Reserve in Spain. We calibrated the model with daily counts recorded in 1984 and 1985, and then used it to predict transit time distributions based on counts of cranes 30 years later (2015–17). The model was calibrated with a mean transit time of 6.5 days observed in 1984/85, consistent with observed values of LOS, and predicted a mean transit time of 5.2 days for the 2015–17 period. The model also predicted an ~6.2× increase of the total migratory passage population of cranes at Gallocanta, which qualitatively agreed with the large increase in the overall population from the 1980s to 2010s. Second, migration dynamics of Eurasian Spoonbills *Platalea leucorodia* were considered during southward migration at two intertidal coastal wetlands in northern Spain from 2002 to 2005. The model well captured the observed differences in transit time between Urdaibai Biosphere Reserve (median transit time of 1.1 days) and Santoña Marshes Natural Park (median transit time of 2.1 days). Transit times of both species were negatively correlated with estimates of annual population sizes. These results indicate that hydrological flow models can provide insights into the migration ecology of waterbirds (or species where regular counts during migration are available), and that LOS is a dynamic decision that can depend on the population sizes of migratory birds.

Keywords: hydrological modelling, length of stay, migration ecology, residence time, total passage population, wetlands.

Most migratory birds stop several times to refuel, rest, roost and recover during their long-distance journeys between breeding and non-breeding areas (Linscott & Senner 2021, Schmaljohann *et al.* 2022). The duration of stopover (length of stay (LOS)) at a site varies widely among species and among individuals of the same species, as well

*Corresponding author.
Email: mark.drever@ec.gc.ca

as between pre- and post-breeding migration seasons, depending on differences in optimal stopover duration for building body-fat reserves and minimizing overall migration duration (Alerstam & Lindström 1990, Weber *et al.* 1994, Alerstam 2011, Schmaljohann *et al.* 2022). LOS is a critical measure for understanding the ecology and management of migratory species (Warnock 2010), and biologists and wildlife managers need practical and cost-effective ways for its estimation. As a population-level measure, the mean value of LOS (LOS_m) provides valuable information to estimate the annual number of birds using a particular site during migration, where the population size is typically estimated as the sum of all daily counts (the total number of 'bird-days') divided by the LOS_m benchmark (Bishop *et al.* 2000, Frederiksen *et al.* 2001, Farmer & Durbian 2006). Further, the variation around LOS_m may provide information about the range of behavioural options available to migrating birds. Therefore, novel ways to estimate LOS_m may inform migration ecology in a variety of ways.

Stopover duration of birds may be expected to vary depending on available resources, disturbance at roosting sites, presence of predators and access to fresh drinking water, and can depend on specific issues such as the body size of the bird relative to the total migration distances. Determining the relationship between population sizes and stopover duration is critical to better understand the ecology of migratory birds, because depletion of resources at stopover sites can contribute to migration mortality and density-dependent population regulation (Newton 2006). These factors may differ between northward and southward migration, which can be fundamentally different ecological events (O'Reilly & Wingfield 1995). Therefore, avian ecologists often require some basic understanding of average LOS to link changes in conditions at migration stopover sites to their population-level consequences.

A variety of methods exist to estimate stopover duration, including methods based on capture–resighting data on individually marked birds (Roques *et al.* 2021), or on devices such as satellite transmitters (Kaiser 1999), GSM/GPRS loggers, and light-level and multi-sensor geolocations (Liechti *et al.* 2018, Briedis *et al.* 2020, Delancey *et al.* 2020). Methods based on migration monitoring, that is, daily counts of birds, offer some promise to inform migration ecology, including ways to quantify timing of migration, number of birds staging and intensity of birds passing through primary migratory corridors, e.g. using estimates of passage population sizes from weather radar (Horton *et al.* 2019a, 2019b, Weisshaupt *et al.* 2021). The use of bird abundance data collected at daily or regular intervals can provide valuable information on LOS if appropriate modelling techniques are applied.

Drever and Hrachowitz (2017) explored the potential of hydrological flow models (Botter *et al.* 2011, Rinaldo *et al.* 2015) to integrate time series of bird counts and estimate stopover duration for migrating birds, based on counts of migrating Western Sandpiper *Calidris mauri* and Dunlin *Calidris alpina* (order Charadriiformes) at two sites on the Pacific coast of Canada. Drever and Hrachowitz (2017) used a hydrological transport model originally designed to describe how water is stored in and released from a system over time. Hydrological flow models characterize a water flow process through a water catchment by quantifying the inflow J, outflow O and storage S during each time step t of a study period. The amount of time that water spends in the system is referred to as the transit time p_T. At each time step t, water in the system can be composed of varying proportions with different ages T, depending on when the various inflows $J[t]$ occurred, and therefore estimating mean transit time $p_{T,\text{m}}$ requires integrating across the entire time series of inputs $J[t]$, outflows $\text{O}[t]$ and storage $S[t]$. Recent advancements in hydrological modelling (Botter *et al.* 2011, Rinaldo *et al.* 2015) achieve this integration through a cohesive framework based on the twinned concepts of the Storage Age Selection (SAS) function ω and the transit time distribution (TTD). The SAS function ω (Rinaldo *et al.* 2015) determines how the storage contents with different ages are sampled (selected) to form the outflow $\text{O}[t]$, i.e. is the outflow composed of 'younger' water or is it primarily 'older' water that has been in the system for longer? The TTD is the probability density function (like a histogram) that describes the full age distribution of the output $\text{O}[t]$ at each time step, that is, what are the age ranges for the water being released at each time step? The TTD is linked to the age composition of the storage $S[T]$ through SAS function ω by a set of differential equations (equations 3–8 in Drever & Hrachowitz 2017). The TTD can then be integrated over the entire time series, from which the mean transit time $p_{T,\mathrm{m}}$ can be calculated to provide a basic summary of the transport behaviour (Sprenger *et al.* 2019).

These components of hydrological flow have direct analogues in bird migration through a stopover site, where inputs J can describe the number of birds arriving, outflow O is the number of birds leaving, storage S is the daily count and transit time is the measure of LOS. In a proof-of-concept study, Drever and Hrachowitz (2017) used this model to analyse historical count data and explore changes in transit time of two species of sandpipers. Drever and Hrachowitz (2017) used this hydrological approach described above with the adaptation to use 'net flow', i.e. the differences between successive counts. Monitoring studies of migrating birds at stopover sites typically only include the storage $S[t]$ information (the daily counts of birds), and therefore the modelling approach uses measures of net flow to set limits on the possible inflows $J[t]$ and outflows O[t] at each time step. The continued application of hydrological models to quantify migration processes and estimate stopover duration from count data on different bird species may enable avian ecologists to identify knowledge gaps, make predictions about future states, support conservation of stopover sites, and make further inferences about changes in stopover duration from historical count data or in situations where other methods (e.g. telemetry methods) are not available or not logistically feasible. Quantifying migration processes allows us to assess the relationship between stopover duration and population size, such that scenarios of population change can be explored in the absence of field data on residence time (e.g. through telemetry studies), a situation commonly encountered in the adaptive management of wetlands.

In this study, we used the approach in Drever and Hrachowitz (2017) to model migration patterns of two common European species: the Common Crane *Grus grus* (order Gruiformes) and Eurasian Spoonbill *Platalea leucorodia* (order Pelecaniformes) during their migrations through the Iberian Peninsula (southwestern Europe). Our objectives were (1) to broadly assess whether methods to quantify water flow through a catchment can be adapted to model bird migration by fitting the model to bird count data and comparing its fitted values to independent data from the same systems, and (2) to expand the use of the Drever and Hrachowitz (2017) approach by using its outflow predictions to derive a measure of total passage population, thereby using the model as a tool to explore quantitative relationships between LOS and population size. In the case study of Common Cranes, we calibrate the model with available information on LOS and bird counts and then apply it to predict LOS based on later time series after a period of rapid population growth. We therefore can ask the model to predict whether this change has resulted from more birds using the site, longer transit times or both. In the case study of Eurasian Spoonbills, we calibrate the model with available information on LOS and bird counts at two different sites and then assess how its performance can vary among stopover locations by comparing its predicted values with independent data sources. In these case studies, we use the model as a descriptor of the system to generate hypotheses about the behaviour of birds at two sites that have different abundances of birds during migration. Additionally, in a series of simulations, we assess how the model can replicate transit times $p_{T,\mathrm{m}}$ derived from time series of counts where the underlying distributions of LOS are known (Appendix S1).

METHODS

Study system 1: Migration of Common Cranes in Gallocanta wetland

Common Cranes undergo long migrations from non-breeding areas in southwestern Europe, north Africa and south Asia to breeding areas in the northern Palaearctic. The western population of this species migrates within the East Atlantic Flyway using a migratory route that crosses a set of traditional stopover/staging sites in western Europe (Prange 2012, Prange & Ilyashenko 2019). The Gallocanta Nature Reserve is an endorheic, saline wetland with a water surface of approximately 1330 ha in central Spain (40°58′N, 1°30′W, 990 m above sea level) and provides a major stopover site along this route (Fig. 1). During the northward migration from late February to March to their breeding sites, Common Cranes use Gallocanta as a staging area, which has a unique position in the migratory route, being the largest shallow wetland providing suitable habitat for Common Cranes before crossing the Pyrenees mountains (Alonso *et al.* 1994). The core

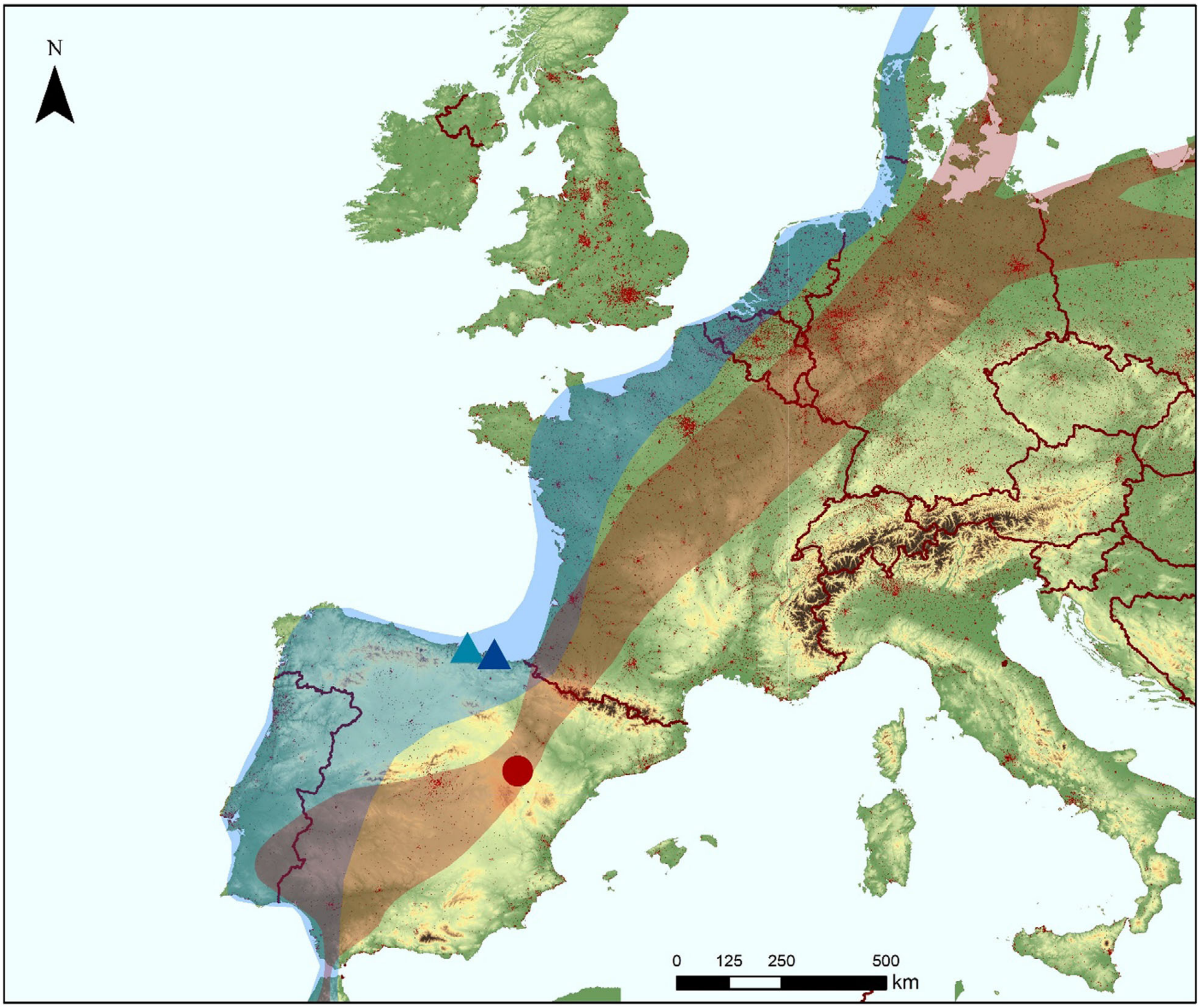

Figure 1. Locations of study sites in Spain. Red circle indicates location of Gallocanta Nature Reserve, where thousands of Common Cranes *Grus grus* stop over during northward migration. Red swathe indicates general migratory route of Common Cranes. Blue triangles indicate locations of Urdaibai Biosphere Reserve and Santoña Marshes Natural Park, where Eurasian Spoonbills *Platalea leucorodia* stop over during southward migration. Blue swathe indicates general migratory route of Eurasian Spoonbills.

migration period is concentrated in approximately 30 days from 15 February to 15 March. We extended the study timeframe by one fortnight before and after the main migration period to account for some early or late migrants, as well as seasonal variability in the timing of the core period (Alonso *et al.* 1987, 1990a, 1990b).

Observers counted both roosting and departing Common Cranes in Gallocanta daily between February and March of 1984 and 1985 (Alonso *et al.* 1987), and this study provided the daily measures of abundance, number of arriving and departing birds, and average LOS. Daily abundance at Gallocanta was calculated as the higher of two daily counts: the dusk count, when Common Cranes arrived at the roost, and the dawn count when cranes left the roost the following morning. We assume that counts had minimal observation error, given that Common Cranes are large birds counted on an open habitat.

Common Crane numbers at Gallocanta increased steadily from the 1980s to the 2010s. Average counts of Common Cranes at the Gallocanta study site averaged ~5000 birds in the mid-

1980s (Alonso *et al.* 1987). Abundance increased in the 1990s to ~12 000 birds, and then to ~28 000 birds in the mid-2000s (Gobierno de Aragón, unpublished data).

Additionally, observers stationed at mountain vantage points counted departing Common Cranes, and these counts provided an independent measure of outflow. The model's transit time was calibrated with the LOS values calculated by Alonso *et al.* (1987). On average, Common Cranes were staying for 8 and 5 days in Gallocanta during the spring migrations of 1984 and 1985, respectively, where LOS was calculated as the difference between mean arrival dates and mean departure dates (Alonso *et al.* 1987).

From 2015 to 2017, the Common Cranes roosting at Gallocanta were not counted daily but once per week by the regional wildlife services (Gobierno de Aragón, unpublished data). Birdwatchers provided a few additional censuses. Wildlife services did not count the daily outflow, and therefore no outflow information was available. We had one measure of LOS during this period based on Common Cranes marked with GPS tags, which spent 1.5 days in Gallocanta (Kaack & Nowald pers. comm.).

We also used independent information on total population sizes of Common Cranes, separate from the migration counts, which was available from surveys conducted in the wintering grounds. This information indicated that Common Cranes exhibited considerable changes in western Europe from the 1980s to the 2010s. The population size increased 5.6× from 40 000–50 000 birds wintering in the Iberian Peninsula and Morocco in 1984/85 (Alonso *et al.* 1986, 2016), to 218 000–287 000 birds leaving Spain through the Pyrenees mountains in 2015–17 (Mooser & Woutersen 2015, Román *et al.* 2016, Molina *et al.* 2017). A summary of information sources of modelling migration dynamics of Common Cranes is available in Table S1. As total population sizes increased, so did the number of Common Cranes at the Gallocanta study area, with nearly all birds that spent the winter in Iberia and Northern Africa stopping at Gallocanta during their spring migration (Fernández-Cruz *et al.* 1981, Bautista *et al.* 1992, Román 2022). Due to its unique position along the flyway, the number of birds at Gallocanta should be directly related to the total population sizes, and the increase of the total number of birds predicted by the hydrological model can be compared with independent measures of Common Crane population size based on birds wintering south of the study site.

Study system 2: Eurasian Spoonbills at Santoña and Urdaibai wetlands

Eurasian Spoonbills (hereafter Spoonbills) are a widespread waterbird species in Europe, Asia and Africa. In Europe, Spoonbills had a breeding population of ~4800 pairs during the early 2000s, of which ~1600 pairs comprised the North Atlantic population (Triplet *et al.* 2008). The majority (>95%) of these birds migrate southward through northern Spain to spend the non-breeding season in the Iberian Peninsula or northwestern Africa (Lok *et al.* 2013). We considered counts of Eurasian Spoonbills during southward migration at two coastal sites in northern Spain (Fig. 1): Santoña Marshes Natural Park and Urdaibai Biosphere Reserve (65 km distance between the two sites). Santoña Marshes and Urdaibai are designated as Ramsar sites and Special Protection Areas because of their roles for Spoonbills during migration. These estuarine wetlands span 1250 and 250 ha, respectively, of effective intertidal areas for foraging birds (Navedo & Garaita 2012). The two sites are strategically situated for Spoonbills migrating southward between breeding grounds in the Netherlands and France towards non-breeding grounds in southwestern Iberia and northwestern Africa (Triplet *et al.* 2008). Santoña and Urdaibai are tidal wetlands located right before crossing 1000 km through continental Spain, where very few stopover/staging wetlands are available, until reaching the southwestern coast where birds stop over again before continuing to Africa, or can remain for the winter (Piersma *et al.* 2021). Santoña Marshes is a key site for Spoonbills (Triplet *et al.* 2008), and 30–40% of this breeding population uses Santoña Marshes to refuel during the southward (autumn) migration (Navedo *et al.* 2010a). Urdaibai has also been identified as an important site during southward migration (Triplet *et al.* 2008), and can support hundreds of birds throughout this period, representing c. 3–10% of the population (Del Villar *et al.* 2007).

Numbers of Spoonbills using both areas were censused on a continuous basis from 9:00 AM to 8:00 PM during more than 28 consecutive days in September throughout 4 consecutive years from 2002 to 2005 (Navedo & Garaita 2012). Counts of Spoonbills were conducted at dawn and dusk from hills overlooking the entire estuaries. At both study areas, in addition to the dawn and dusk counts, observers were able to directly observe birds leaving the estuary throughout the day (Navedo & Garaita 2012), which provided a measure of outflow. We assume that the majority of birds that left did not return that same migration period, and that there was minimal observation error on these counts, given that they are large birds censused on an open habitat.

Independent measures of $\mathrm{LOS_m}$ of Spoonbills in Santoña were available from ringing studies conducted during September in the 4 consecutive years (2002–05) based on 974 re-sightings of 263 PVC-ringed birds (Navedo *et al.* 2010b). Minimum $\mathrm{LOS_m}$ was defined as the time elapsed between first and last observation of a bird in the estuary during each migration season, and $\mathrm{LOS_m}$ varied from 1 to 3 days over the study period. Resighting probability of birds that stopped over 3 days or more was 0.89 ± 0.01 standard error, and did not differ between years (Navedo *et al.* 2010b), and therefore we assumed minimum $\mathrm{LOS_m}$ approached real $\mathrm{LOS_m}$. For Urdaibai, we used a value of 1 day for $\mathrm{LOS_m}$ to calibrate the model (see below), because 95% of Spoonbills that stop over at that site rest for some hours and then resume migration (Navedo & Garaita 2012). A summary of information sources of modelling migration dynamics of Spoonbills is available in Table S1.

Hydrological modelling approach

The Drever and Hrachowitz (2017) hydrological approach models migration dynamics as a Monte Carlo stochastic simulation, wherein we generate many joint outcomes of a random process, and we then observe the behaviour of response variables that are functions of these outcomes. These behaviours are characterized by the probability density functions of response variables. In our case, the focal response variable is the TTD, from which we can derive the mean transit time $p_{T,\mathrm{m}}$. The model has two simple inputs: a time series of daily (or regular) counts as a measure of storage $S[t]$, and a time series of net flow, that is, the sequential difference between successive counts of birds, $S[t] - S[t + 1]$. The outputs of the model are a set of time series that represent the posterior sampling distributions of inflow $J[t]$ and outflow $\mathrm{O}[t]$, as well as the SAS function ω, and the TTD[T]. Note that we use the term ‘transit time’ to denote model-calculated values, and ‘length of stay’ (LOS) to denote values obtained from field studies, although both sets of values are meant to represent the stopover duration of birds at migration sites.

Calibrating the hydrological model

The model calibration involves several steps, and it requires independent estimates of LOS along with time series of observed counts. First, we generated random time series ($k = 10^6$) that characterized $S[t]$, inflow $J[t]$, outflow $\mathrm{O}[t]$ and their associated uncertainties. For $S[t]$, the observed bird counts were randomly sampled from the observed values ±25% to incorporate an assumed observation error (Rappoldt *et al.* 1985). These resulting $S[t]$ series then served as a basis to construct the time series of $J[t]$ and $\mathrm{O}[t]$ for each iteration, wherein we used the sequential change in the number of birds (the ‘net flow’) to define the upper and lower bounds of possible inflow $J[t]$ and outflow $\mathrm{O}[t]$ rates for each time step in each model iteration, following equations 10–15 in Drever and Hrachowitz (2017).

Second, we generated k iterations of the SAS function ω that defines how a catchment selectively removes water of different ages from storage that becomes the outflows, that is, how long birds remain at a stopover site and the patterns to which they leave again. We used a beta function $B(\alpha,\beta)$ as the basis for the SAS function ω (equation 16 in Drever & Hrachowitz 2017). The beta function is controlled by the α and β parameters and allows for a wide diversity of shapes (see fig. 4 in Drever & Hrachowitz 2017), including a flat SAS function ω with no storage age preference ($\alpha = 1$, $\beta = 1$), preference for younger ages ($\alpha < 1$, $\beta > 1$) and preference for older ages ($\alpha > 1$, $\beta < 1$). For each of the 10^6 model realizations, α and β were sampled from the uniform prior distributions with very wide lower and upper bounds ($0.0001 < \alpha < 20$; $0.0001 < \beta < 100$). The TTD is then calculated for each iteration by combining the k time series of $S[t]$, $J[t]$ and $\mathrm{O}[t]$ with the k SAS function ω using differential equations 3–8 in Drever and Hrachowitz (2017) to derive 10^6 solutions to the integration, and $p_{T,\mathrm{m}}$ was calculated from the TTD (equation 17 in Drever & Hrachowitz 2017).

In a third step during the calibration, only solutions that were able to replicate the observed patterns in abundance and stopover duration were retained. Solutions that met criteria of matching independent population estimates (see below) and those solutions that resulted in $p_{T,\mathrm{m}}$ values that were within ±25% of the known $\mathrm{LOS_m}$ were retained. For the Common Cranes, we discarded solutions where predicted passage population sizes, estimated as the sum of all daily predicted inflows, $\Sigma J[t]$, exceeded plausible upper limits of incoming individuals of 40 000 and 50 000 birds, respectively (Alonso *et al.* 2016). In a last step, solutions that exceeded the maximum daily number of 20 000 arriving individual birds were also discarded. For the Spoonbills, the model calibration was based only on the known $\mathrm{LOS_m}$ estimates. Following calibrations, plots were made of the resulting time series of storage $S[t]$, inflow $J[t]$, outflow $\mathrm{O}[t]$, the SAS function ω and the TTD for interpretation. We note the inherent circularity to this calibration approach, and caution is needed when the approach is used for hypothesis testing. However, our intent was to provide a quantitative description of a migration system and draw inference from the shape of the SAS function ω and TTDs about migration behaviours.

Using the hydrological model for predictions

For the Common Cranes, hydrological model parameters were calibrated with data from the 1984/85 period, and we then used the model to predict transit times based on the observed counts from 2015 to 2017. The same procedures described above are used to derive random time series of storage $S[t]$, inflow $J[t]$ and outflow $\mathrm{O}[t]$ based on the counts conducted from 2015 to 2017, and these time series are combined with SAS function ω obtained from the posterior distributions of parameters α and β from calibration years 1984 and 1985. The 5th/95th centiles of this prior distribution were $\alpha = 1.45/19.31$ and $\beta = 0.0013/0.036$. This approach assumes that the migration dynamics have remained similar during the two periods (e.g. that outflow birds are mostly birds that have been there the longest; see Results), and the main change is the larger numbers of birds observed from 2015 to 2017. The subsequent Monte Carlo approach with 10^6 realizations then sampled from these updated uniform prior uniform distributions to derive TTDs and mean transit times $p_{T,\mathrm{m}}$ for years 2015 to 2017.

Testing the hydrological model results

To test the model predictions, we compared the outflow $\mathrm{O}[t]$ values to the independent counts of departing birds that were available from field studies of Common Cranes in 1984 and 1985 (Alonso *et al.* 1987) and Spoonbills from 2002 to 2005 (Navedo & Garaita 2012). For each site/year combination, a Pearson's correlation coefficient was calculated between $\mathrm{O}[t]$ and the corresponding number of birds observed departing on that date.

We also derived estimates of passage population, that is, the total number of individual birds that used the stopover site, by summing the median influx $J[t]$ values for each time step, such that total passage population = $\Sigma\ J[t]$ for each migration period, and then compared the proportional change between the calibration and prediction periods in passage population with the estimates of total population sizes available from the non-breeding grounds.

To examine the relationship between transit times and annual abundances of Spoonbills, we obtained estimates of the total adult population derived from the main breeding grounds (number of breeding pairs ×2 in the Netherlands plus France) for 2002–2005, which varied from 2800 to 3800 birds (Werkgroep Lepelaar unpubl. data, Marion 2013). These estimates served as an independent measure of the potential number of adult birds that stop over at Urdaibai or Santoña each year. To evaluate the relationship between transit times and overall abundance of birds, we fit a general linear model using the eight median values of transit time (4 years × 2 sites) as the response variable, with site (Urdaibai/Santoña) and total annual adult population (scaled) as explanatory variables. An interaction term between the site and population size was initially considered, but was not statistically significant, and so was excluded in the regression model. We recognize the small sample size ($n = 8$) of this regression, and we present these results as preliminary.

RESULTS

Common Cranes

Daily counts of Common Cranes at Gallocanta occurred from 27 January to 31 March, and varied widely from 1 bird to 28 878 birds, with median values of 2926 birds in 1984 and 3130 birds in 1985

(Fig. 2). For the prediction period from 2015 to 2017, counts varied from 54 to 82 906 birds, with median values of 15 300 birds in 2015; 9973 birds in 2016; and 8314 birds in 2017 (Fig. 2).

The migration dynamics of Common Cranes during the springs of 1984 and 1985 were well characterized during the calibration of the hydrological model. The SAS ω functions were based on α and β parameters with narrow feasible ranges, as illustrated by the 5th/95th centile range ($IQR_{5/95}$) of their posterior distributions, which resulted in a J-shaped SAS function ω with a left-tail negative skew (Fig. 2d). This shape for the SAS function indicated a preferential selection for older 'ages', that is, of the birds present at the wetland at a given time, the individuals leaving tended to be composed primarily of birds that had arrived the longest time ago. A leftward shift occurred in the curve of the SAS function from 1984 to 1985 (visible in the insets of Fig. 2d), resulting in a difference in transit time distributions between 1984 and 1985 (Fig. 2e). The results suggest that in 1984, Common Cranes had an average transit time $p_{T,\mathrm{m}}$ that ranged from 6.8 to 8.5 days (median 7.9 days), and some individuals may have remained at the site for up to 20 days. In contrast, in year 1985 average $p_{T,\mathrm{m}}$ values ranged from 4.4 to 5.4 days ($IQR_{5/95}$, median = 5.0 days), and almost all birds had left the site after ~15 days. These average $p_{T,\mathrm{m}}$ values correspond well with the observed LOS values of 8 days in 1984 and 5 days in 1985 (Alonso *et al.* 1987).

Migration dynamics for the prediction period (2015–17) were characterized by an SAS function ω that was again a left-tailed J-shape (Fig. 2d, single ω function for all years). Model predicted

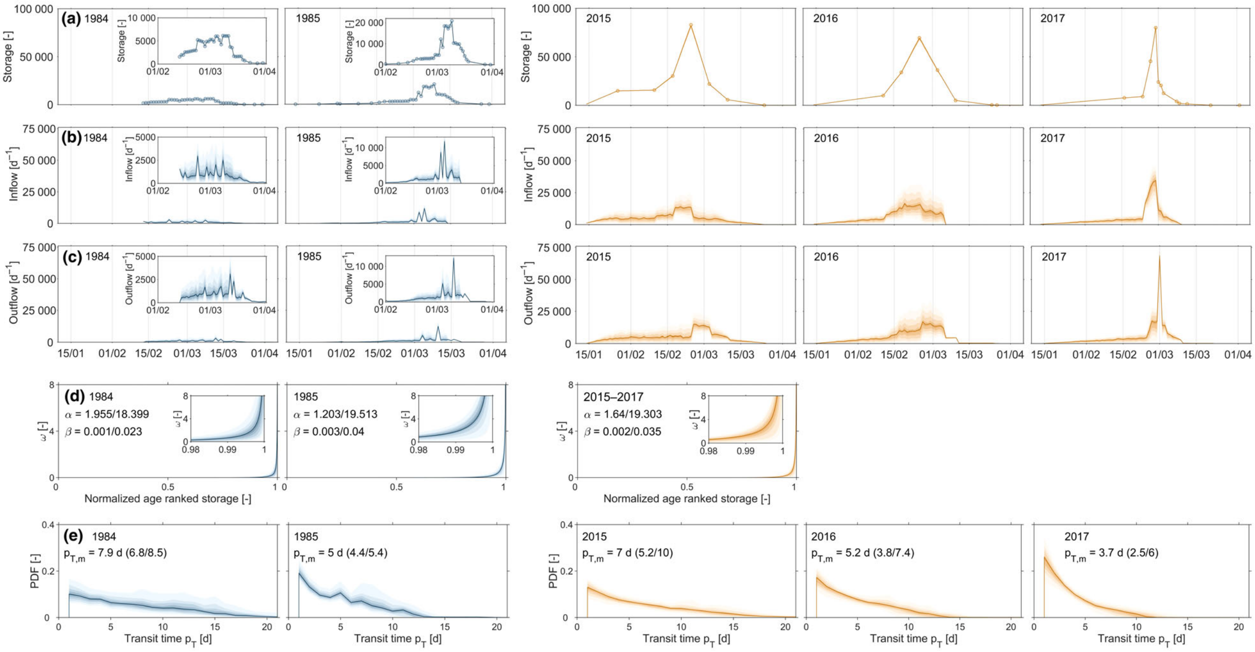

Figure 2. Migration dynamics of Common Cranes *Grus grus* at Gallocanta Nature Reserve, Spain. Time series of (a) daily bird counts (or Storage) S randomly sampled from the observed values (dots) of $S \pm 25\%$, (b) daily bird arrival (or Inflow) rates J, randomly sampled between J_{min} and J_{max} as obtained from equation 10 in Drever and Hrachowitz (2017), and (c) daily bird departure (or outflow) rates O, randomly sampled between O_{min} and O_{max} as obtained from equation 11 in Drever and Hrachowitz (2017). Blue and orange shades indicate the 5th/95th centile range of calibration and prediction values, respectively. Note the different scales between calibration and prediction series. The black lines in (b) and (c) indicate the time series associated with the transit time $p_{T,\mathrm{m}}$ that best describes the length-of-stay benchmark ($\mathrm{LOS_m}$) for the respective year. The full list of symbols and parameters used to estimate the transit and transit times for calculating length of stay of migrating birds are provided in table 1 of Drever and Hrachowitz (2017). (d) Storage Age Selection (SAS) function (or ω) for each year, with median values of α and β, and the 5th/95th centile range of their posterior distribution for each year. (e) Marginal transit time distributions p_T for each year (i.e. the outflow-weighted averages of the individual daily transit time distributions). The shaded areas in (a)–(e) were constructed from the weighted likelihood measures of each model realization using equation 17 (Drever & Hrachowitz 2017).

transit times during the prediction period were similar to or shorter than during the calibration period: $p_{T,\mathrm{m}}$ was 7, 5.2 and 3.7 days, respectively for the years from 2015 to 2017. The shorter transit time in 2017 coincided with a very short migration period of c. 10 days (Fig. 2a). The shape of the SAS function ω indicated that, of the Common Cranes present at the wetland at a given time, the outflow was composed primarily of birds that had arrived the longest time ago.

The outflow O[t] values predicted from the model were positively and significantly correlated with independent counts of departing birds (see Fig. S1) during both 1984 ($r = 0.63$, $P < 0.001$) and 1985 ($r = 0.94$, $P < 0.001$).

We calculated total passage populations during the calibration period using the model outputs as the total annual sums of all predicted inflows (36 918 birds in 1984 and 65 005 birds in 1985). Thirty years later, the model predicted a 6.2× increase in the total passage population during the prediction period: total sums of inflow values were 337 910 in 2015, 334 514 in 2016 and 280 500 in 2017 for Common Cranes. The 6.2× increase was qualitatively like the previous change in the estimates of total passage populations (Fig. 3), with the two measures being strongly correlated ($r = 0.95$, $n = 5$, $P = 0.01$), although the model tended to predict larger values than the previously estimated total passage populations (Alonso *et al.* 1987, Mooser & Woutersen 2015, Román *et al.* 2016, Molina *et al.* 2017).

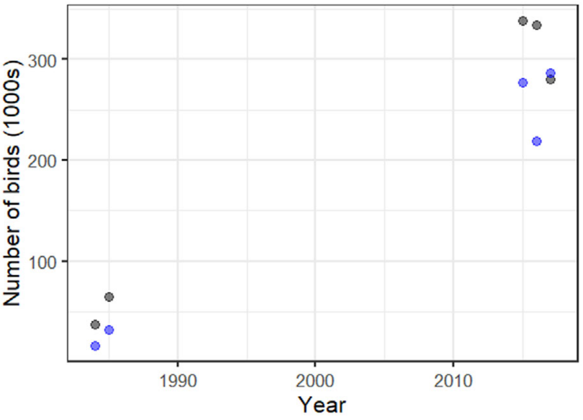

Figure 3. Total passage population of Common Cranes *Grus grus* during northward migration at Gallocanta Nature Reserve, Spain, from previous estimates (blue symbols) or calculated from hydrological model (black symbols).

Eurasian Spoonbills

Migrating Spoonbills were much less numerous at Urdaibai (Fig. 4) than at Santoña (Fig. 5): median counts of birds leaving daily from Santoña Marshes ranged between 46 and 88 Spoonbills from 2002 to 2005, with maxima from 143 to 497 birds. In contrast, median counts of Spoonbills leaving Urdaibai were one or two birds, with maxima of 5–94 birds, from 2002 to 2005. The flow dynamics of migrating Spoonbills differed between Urdaibai and Santoña sites (Figs 4 & 5). At Urdaibai, α and β parameters for the SAS function ω had wide values for each year (Fig. 4d), resulting in variable functions. For each year, the resulting transit distributions indicated that all birds had departed by 3 days, with an average $p_{T,\mathrm{m}}$ values that ranged from 1 to 1.2 days (median 1.1 days). At Santoña, dynamics were more consistent from year to year, with α and β parameters with narrow feasible ranges in 2002, 2003 and 2005, which resulted in a J-shaped SAS function ω with a left-tail negative skew (Fig. 5). In 2004, the α and β parameters had more variable ranges, and the SAS functions ω had highly variable forms. The balance of the volume and flow rates resulted in estimated $p_{T,\mathrm{m}}$ values for Spoonbills at Santoña that ranged from 1.6 to 2.2 days (median 2.1 days).

The outflows predicted from the model were positively correlated with independent counts of departing Spoonbills, with details varying between the two sites (see Fig. S2). At Urdaibai, correlations between outflow values O[t] and independent counts of departing Spoonbills were strongly positively correlated for 2004 and 2005 ($r = 0.76$ to $r = 0.87$, $P < 0.001$), moderate for 2002 ($r = 0.47$, $P = 0.0087$) and weakly positive for 2003 ($r = 0.18$, $P = 0.36$). At Santoña, O[t] values showed significant strong positive correlations for all years ($r = 0.75$ to $r = 0.95$, $P < 0.001$), with correlations in 2002 being somewhat weaker ($r = 0.45$, $P = 0.01$).

Total annual adult populations estimated from surveys conducted on the breeding grounds from 2002 to 2005 ranged between 2872 and 3800 Spoonbills. Annual $p_{T,\mathrm{m}}$ values for Urdaibai and Santoña were negatively correlated with total annual populations (Fig. 6). The general linear model depicting variation in transit time had a statistically negative parameter value for total population size

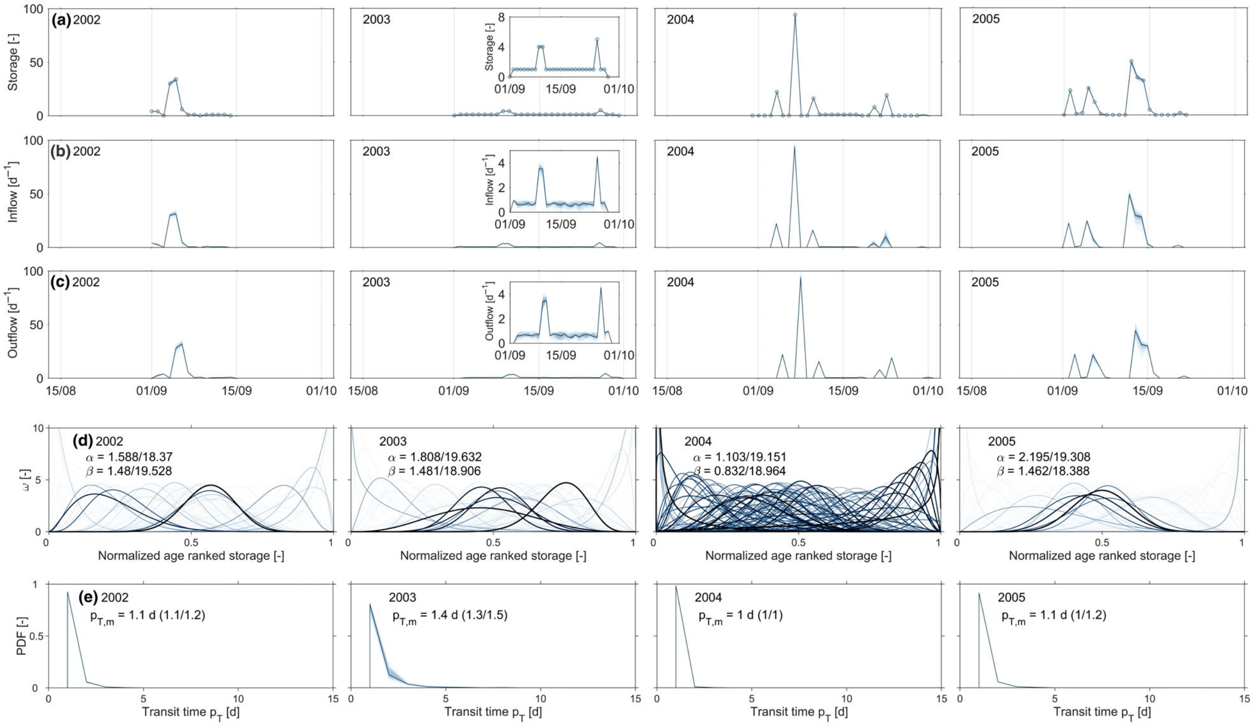

Figure 4. Migration dynamics of Eurasian Spoonbills *Platalea leucorodia* at Urdaibai Biosphere Reserve, Spain. Conventions are as in Fig. 2. Time series of (a) daily bird counts (or Storage) S randomly sampled from the observed values (dots) of $S \pm 25\%$, (b) daily bird arrival (or Inflow) rates J, randomly sampled between $J_{\min}$ and $J_{\max}$ as obtained from equation 10 in Drever and Hrachowitz (2017), and (c) daily bird departure (or outflow) rates O, randomly sampled between $O_{\min}$ and $O_{\max}$ as obtained from equation 11 in Drever and Hrachowitz (2017). Blue shades indicate the 5th/95th centile range of calibration values respectively. The black lines in (b) and (c) indicate the time series associated with the transit time $p_{T,\mathrm{m}}$ that best describes the length-of-stay benchmark (LOS$_\mathrm{m}$) for the respective year. The full list of symbols and parameters used to estimate the transit and transit times for calculating length of stay of migrating birds are provided in table 1 of Drever and Hrachowitz (2017). (d) Storage Age Selection (SAS) function (or ω) for each year, with median values of α and β, and the 5th/95th centile range of their posterior distribution for each year. (e) Marginal transit time distributions p_T for each year (i.e. the outflow-weighted averages of the individual daily transit time distributions). The shaded areas in (a)–(e) were constructed from the weighted likelihood measures of each model realization using equation 17 (Drever & Hrachowitz 2017).

($\beta_{\mathrm{pop}} = -0.15$, standard error = ±0.048, $t = -3.14$, $P = 0.026$).

DISCUSSION

We tested hydrological concepts from SAS functions ω to describe migration patterns and found transit time $p_{T,\mathrm{m}}$ estimates similar to LOS estimates from field studies in Common Cranes and Eurasian Spoonbills. The present study extended the potential of the hydrological concept of ω functions outlined in the Drever and Hrachowitz (2017) model – originally applied to two small shorebird species (*Calidris* sp.) – by considering the particularities of two large waterbird species. It also provided insights into relationships between abundances at migration sites and stopover duration. This model stands as an instrumental tool for migration studies based on daily or regular counts of unmarked populations. It provides a way to integrate measures of abundance with net flow, that is, changes between consecutive counts, from which to derive measures of total passage populations and residence times in wetlands and species with very different characteristics and requirements.

Common Cranes

Our model suggested that a negative relationship occurred between bird abundance and transit time for Common Cranes at Gallocanta during both

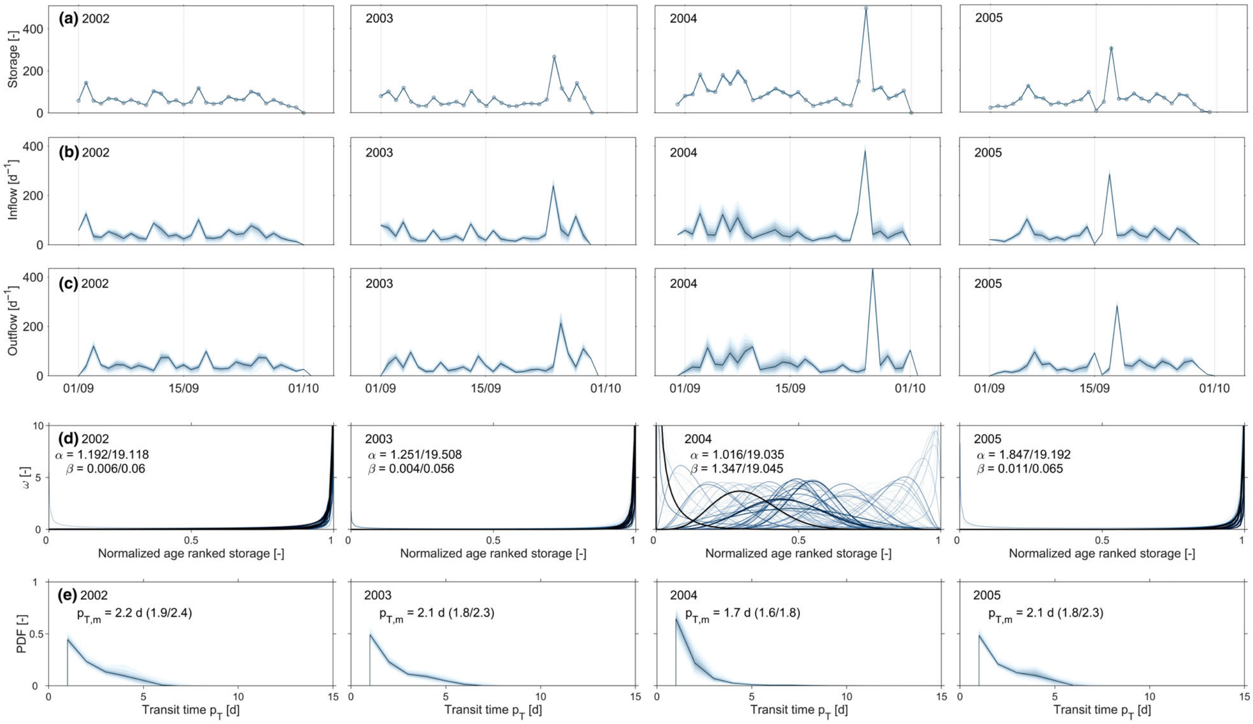

Figure 5. Migration dynamics of Eurasian Spoonbills *Platalea leucorodia* at Santoña Marshes Natural Park, Spain. Time series of (a) daily bird counts (or Storage) S randomly sampled from the observed values (dots) of $S \pm 25\%$, (b) daily bird arrival (or Inflow) rates J, randomly sampled between J_{min} and J_{max} as obtained from equation 10 in Drever and Hrachowitz (2017), and (c) daily bird departure (or outflow) rates O, randomly sampled between O_{min} and O_{max} as obtained from equation 11 in Drever and Hrachowitz (2017). Blue shades indicate the 5th/95th centile range of calibration values respectively. The black lines in (b) and (c) indicate the time series associated with the transit time $p_{T,\text{m}}$ that best describes the length-of-stay benchmark (LOS$_\text{m}$) for the respective year. The full list of symbols and parameters used to estimate the transit and transit times for calculating length of stay of migrating birds are provided in table 1 of Drever and Hrachowitz (2017). (d) Storage Age Selection (SAS) function (or ω) for each year, with median values of α and β provide the 5th/95th centile range of their posterior distribution for each year. (e) Marginal transit time distributions p_T for each year (i.e. the outflow-weighted averages of the individual daily transit time distributions). The shaded areas in (a)–(e) were constructed from the weighted likelihood measures of each model realization using equation 17 (Drever & Hrachowitz 2017).

study periods. During the calibration period (1984/85), an observed daily mean of 3426 Cranes stayed 8 days on average in spring 1984 (Alonso *et al.* 1990b). When the daily population counts nearly doubled up to 6497 birds in spring 1985, the transit time decreased to 5 days. The difference in the migration patterns between the 1984 and 1985 passages was attributed to extrinsic weather conditions, especially rain, cloudiness and strong headwinds (Alonso *et al.* 1990a, 1990b). Here we propose a second, not mutually exclusive, explanation: according to the hydrological model, the higher abundances seen in 1985 may have resulted in shorter transit times and greater flow rates relative to 1984 due to an intrinsic population regulation process. During the prediction period (2015–17), much higher abundances of Common Cranes were observed, with median counts of 9973 birds (Fig. 2), coincident with predicted transit time $p_{T,\text{m}}$ values ranging from 3.7 to 7.0 days, again suggesting a link between LOS and abundance of migrating Cranes.

Several mechanisms could explain the inverse relationship between spring stopover duration and population size of Common Cranes. An increase in population size could lead to disturbances at the Gallocanta roost sites, prompting the birds to reduce transit time. This mechanism is plausible, especially when the water levels in this endorheic wetland are low. Incidentally, water levels during the two periods studied here (1984/85: model calibration; 2015–17: model prediction) were in the lower range of the historical series (fig. 11 in Luna *et al.* 2016; fig. 1 in Orellana-Macías *et al.* 2020).

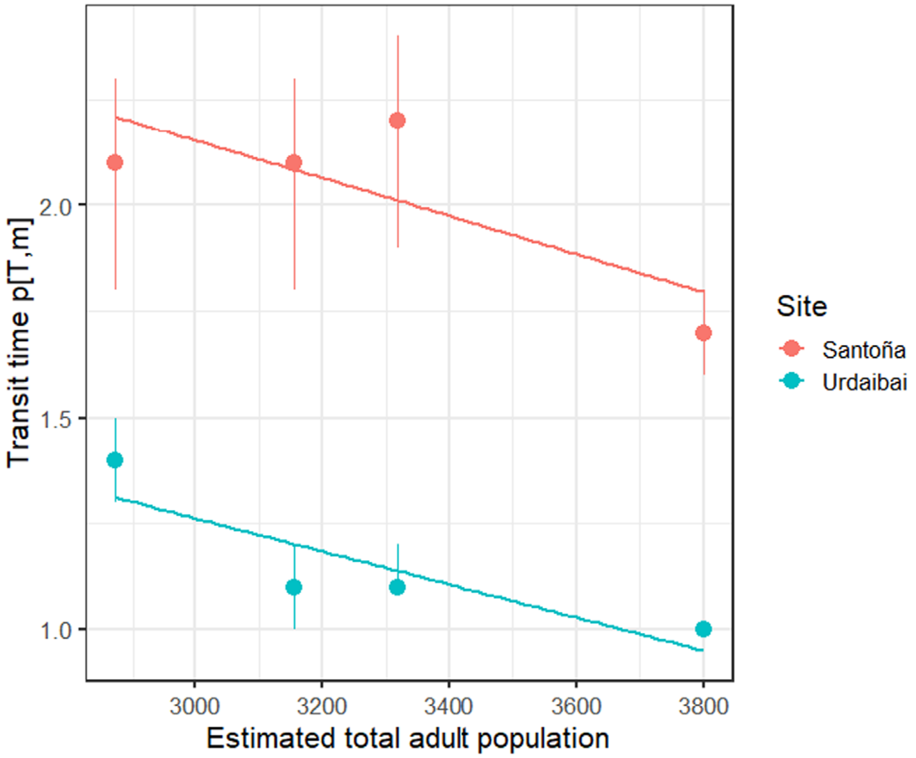

Figure 6. Estimated length of stay (median transit time with 95% confidence limits) of Eurasian Spoonbills during southward migration at two sites (Santoña Marshes Natural Park and Urdaibai Biosphere Reserve) in northern Spain, as a function of total breeding populations, 2002 to 2005. The lines illustrate predicted values from a General Linear Model.

A large population coupled with low water levels may have accelerated Common Crane passage in the study area, and the larger daily population during spring migrations from 2015 to 2017 (c.28000 Common Cranes, Gobierno de Aragón, unpublished data) could have further reduced transit time. Our results are supported by short LOS estimates of two individual Common Cranes tagged with GPS transmitters in the mid-2000s. These birds spent ~1.5 days in Gallocanta, based on time differences between arrival and departure, which were 36 h (1.5 days) on average (range: 12–62 h, $n = 4$ migrations (two individuals, two springs each), Kaack & Nowald pers. comm.). It is therefore plausible that an increase in the average daily number of Common Cranes was coupled with the decrease in average stopover duration.

Common Cranes encounter a variety of trade-offs regarding their decisions to shorten or prolong their stopover duration. For example, rain and strong headwinds can impede daily migration departures of Common Cranes (Alonso *et al.* 1987, 1990b). Indeed, the hydrological model captured well the day-to-day variability in storage and outflow values during the calibration period, and it consistently resulted in a J-shaped SAS function ω with a left-tail negative skew, suggesting a biologically realistic pattern where outflow is composed selectively of birds that had been there the longest. Although we could not evaluate the match between model outflow predictions and counts of departing birds during the prediction period from 2015 to 2017, we found that the model characterized the storage (weekly counts) well, provided reasonable values of transit time, and was able to qualitatively capture the six-fold increase in the total migration population. The short-term variability hidden by the weekly counts during the prediction period did not affect the suitability of the hydrological approach to calculate transit times, probably because successive weekly counts showed a coherent seasonal pattern of increasing and then decreasing counts. This observation underscores the need to calibrate the model with counts conducted with higher frequency (i.e. daily counts in the calibration sample) than the expected mean transit time (a few days) to provide reasonable bounds of outflow and inflow rates. Additionally, survey frequency also needs to be optimized within the full purpose of the monitoring programme, e.g. providing sufficient power for trend estimation (Crewe *et al.* 2015).

Eurasian Spoonbills

We considered Spoonbills moving through two sites in northern Spain during their southward migration, in contrast to the northward migration of Common Cranes in the previous case study. Therefore, annual abundances at Urdaibai and Santoña are determined by the overall adult breeding population size as well as their reproductive success. We found a negative correlation between transit time $p_{T,\mathrm{m}}$ values at both wetlands and total annual abundances at breeding areas in France and The Netherlands. Despite this shared temporal pattern, the spatial differences in stopover duration between Urdaibai and Santoña are in opposite directions, that is, Urdaibai had shorter stopover durations and lower abundances of Spoonbills, compared with Santoña. These contrasting patterns probably reflect how the two wetlands are used (Navedo & Garaita 2012). The majority (~80%) of Spoonbills passing through Santoña continue a southwestern trajectory on an inland route (Navedo *et al.* 2010a). This route offers a general scarcity of potential stopover sites towards wintering sites in southwestern Iberia and West Africa. Indeed, Spoonbills wintering in West Africa have longer stopover duration at Santoña, suggesting a staging behaviour by birds that made long 'jumps' between sites (Warnock 2010), in comparison with those wintering in Iberia (Navedo *et al.* 2010b). The remainder (~20%) go westward through a coastal route with plenty of small estuaries, enabling a stopover behaviour by birds that can make small 'hops' between sites (Warnock 2010). This mix of migration strategies at Santoña is reflected in the greater annual variance in $\mathrm{LOS_m}$, which contrasts with the behaviour at Urdaibai, where most Spoonbills remain for <24 h (Garaita & Arizaga 2015), hence following a clear stopover behaviour pattern that did not vary widely from year to year.

In contrast to the Common Crane case study, fitting the hydrological model for the Spoonbills did not always result in well-defined SAS function ω (Figs 4 & 5), especially for the counts at Urdaibai. At Urdaibai, counts of Spoonbills were generally low (Fig. 4), and the mean transit time (~1 day) was very similar to the minimum step length in the model and may therefore represent an especially difficult case to fit the model. At Santoña, larger numbers of birds were recorded over longer time periods than at Urdaibai, and the hydrological modelling suggested a J-shaped SAS function ω with a left-tail negative skew for 3 of 4 years, like the SAS function ω detected for the Common Cranes. In post hoc simulations, we fit the model in a series of both calibration and prediction runs (Appendix S1), and we found that the transit times can be strongly controlled by the structure of the fluctuations rather than differences in SAS function ω, that is, the time series of population and inflow constraints imposed on the model. In these cases, the model can predict the number of birds leaving and serves as quantification of the flow of birds through a study system but does not provide additional information about the age structure of the outflow.

General insights into migration ecology

Along with the original results in Drever and Hrachowitz (2017), this hydrological model has been used to investigate migration dynamics of four different bird species at five wetlands in Pacific North America and western Europe, during both southward and northward migration. In each case, a J-shaped ω function with a left-tail negative skew was the common pattern, indicating that most birds show annual variation around a similar stopover/staging pattern. The J-shape reveals a system that preferably 'releases' older ages in storage, that is, the outflow is composed of birds that have been at the migration site the longest, with little mixing of birds with different residence times. This pattern suggests that most migrating birds stay at a particular wetland for the minimum time possible. Drever and Hrachowitz (2017) speculated that this J-shaped ω function with a left-tail negative skew may be a good default under given conditions, and that, for modelling on future datasets, we could consider narrower limits for the β distribution defining the ω function. However, we would be reluctant to do so without a well-founded theory of the collective bird behaviour that we observed for Common Cranes and Spoonbills, especially given the variability seen for the ω function of Spoonbills at Urdaibai. In particular, the transit time estimates in these test cases have ranged between 1 and 8 days, and it is unknown how well this model would function with data from wetlands with longer stopover durations or from wetlands where birds have a mix of migration tactics, e.g. terminus migration wetlands near wintering grounds that would have both birds that are arriving at their non-breeding destination and birds that are continuing through. Nonetheless, in cases for which a sharply defined research hypothesis or biological expectation for this collective behaviour is expected, we could consider a tentative case for narrowing priors and so be able to make inferences from counts alone without needing ancillary information to prune possible solutions.

This model establishes a robust framework to integrate regular counts of birds, outflow, residence time and total passage populations, offering insights into the ecological underlying processes that determine avian use of wetlands. In the two case studies for Common Cranes and Spoonbills, we found evidence for a negative relationship between stopover duration and the number of birds using the sites in each migration. This pattern indicates the potential for limited resources available at these migration sites. Without relevant environmental covariates, we could not disentangle the underlying mechanisms, or even the cascade of causation, i.e. do birds stay for shorter periods because food is being depleted, or do migration sites with abundant food resources allow birds to refuel faster and support more birds? In general, migrants tend to stay for longer when food is plentiful and move on when food is scarce (see review in Newton 2006). This relationship means that site quality during migration has the potential for density-dependent population regulation (Newton 2004), and it should be explored further. This exploration could be carried out from both sides: more studies to quantify LOS for different species and at different sites, and more research about collective behaviour and environmental conditions at such sites (Flack *et al.* 2022).

Conclusion

In summary, we extended the Drever and Hrachowitz (2017) hydrological concept of the storage age selection functions to model time series counts of Common Cranes and Spoonbills, estimating upper and lower bounds on the net flow of birds entering and leaving a stopover site on, respectively, northward and southward migrations. The hydrological model predicted changes in bird abundances with narrow confidence intervals (Figs 2, 4 & 5), and calculated shorter transit times when we challenged the model with counts of Common Cranes that were four to six times greater in magnitude relative to the calibration data. These studies indicate a pattern where stopover duration was negatively correlated with the total numbers of birds using a wetland during migration, and that the outflow of birds leaving wetlands after stopover or staging behaviour was preferentially composed of birds that had remained there for the longest periods of time.

We thank J. A. Alonso, R. Muñoz-Pulido and F. J. Cantos for their collaboration in Crane counts at Gallocanta Lake. The Crane censuses were financed by the Dirección General de Medio Ambiente (Ministerio de Obras Públicas y Urbanismo, Spain) (1984/85), and by the Department of Agriculture, Livestock and the Environment (Aragón, Spain) (2015–17). J. A. Román, A. Torrijo and J. M. Pueyo provided unpublished updates of population sizes of Common Cranes wintering in Spain and Portugal, and A. Onrubia of northern Africa. Unpublished arrival and departure dates of two GPS-tagged Cranes were provided by G. Nowald and S. Kaack. We also thank I. Ojaste and A. Broniarek for providing additional data of other GPS-tagged Cranes. Thanks to the volunteers for their valuable help during the fieldwork at Santoña. JGN was financially supported to carry out the field work at Santoña by SEO/BirdLife and O.A. Parques Nacionales (belonging to the former Spanish Ministry of the Environment). Counts at Urdaibai were supported by Department of Environment, Territorial Planning, Agriculture and Fisheries of the Basque Government. We thank R. Garaita for allowing the use of the Urdaibai dataset, and P. De Goeij for allowing the use of unpublished information from Werkgroep Lepelaar about annual breeding pairs of Eurasian Spoonbills in The Netherlands. We thank R. Nager, S. Oppel, F. Liechti and P. Battley for kindly reviewing the manuscript. Their comments and insights substantially improved the manuscript. Open Access funding provided by the Environment and Climate Change Canada library.

AUTHOR CONTRIBUTIONS

Mark C. Drever: Conceptualization; writing – original draft; writing – review and editing; project administration; investigation; methodology; visualization; supervision; resources; funding acquisition;

formal analysis; software. **Luis M. Bautista-Sopelana:** Conceptualization; methodology; data curation; investigation; validation; formal analysis; supervision; resources; visualization; writing – original draft; writing – review and editing. **Juan C. Alonso:** Writing – original draft; writing – review and editing; data curation. **Juan G. Navedo:** Conceptualization; writing – review and editing; data curation; visualization. **Markus Hrachowitz:** Conceptualization; investigation; writing – original draft; writing – review and editing; methodology; validation; formal analysis; software; visualization; data curation; supervision.

CONFLICT OF INTEREST

The authors do not have any potential sources of conflict of interest.

ETHICAL NOTE

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

Alerstam, T. 2011. Optimal bird migration revisited. *J. Ornithol.* **152**: 5–23.

Alerstam, T. & Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy, and safety. In Gwinner, E. (ed) *Bird Migration: physiology and Ecophysiology*: 331–351. Berlin: Springer.

Alonso, J.A., Alonso, J.C. & Cantos, F.J. 1986. On the size of the common crane *Grus grus* population migrating through western Europe. *Ornis Fenn.* **63**: 58–59.

Alonso, J.C., Alonso, J.A. & Cantos, F.J. 1987. Crane spring migration over Gallocanta (Spain). *Aquila* **94**: 213–222.

Alonso, J.A., Alonso, J.C., Cantos, F.J. & Bautista, L.M. 1990a. Spring crane *Grus grus* migration through Gallocanta, Spain. 2. Timing and pattern of daily departures. *Ardea* **78**: 379–386.

Alonso, J.C., Alonso, J.A., Cantos, F.J. & Bautista, L.M. 1990b. Spring crane *Grus grus* migration through Gallocanta, Spain. 1. Daily variations in migration volume. *Ardea* **78**: 365–378.

Alonso, J.C., Alonso, J.A. & Bautista, L.M. 1994. Carrying-capacity of staging areas and facultative migration extension in common cranes. *J. Appl. Ecol.* **31**: 212–222.

Alonso, J.A., Alonso, J.C. & Nowald, G. 2008. Migration and wintering patterns of a central European population of common cranes *Grus grus*. *Bird Study* **55**: 1–7.

Alonso, J.C., Alonso, J.A., Onrubia, A., Cruz, C.M., Cangarato, R. & Rocha, P. 2016. Assessing four decades of wintering crane counts in Spain, Portugal and Morocco. Proceedings of the European Crane Conference, 8, 28–37. Conference organized by Friends of Gallocanta (eds.), 10th of November 2014. Gallocanta, Spain.

Bautista, L.M., Alonso, J.C. & Alonso, J.A. 1992. A 20-year study of wintering common crane fluctuations using time-series analysis. *J. Wildl. Manag.* **56**: 563–572.

Bishop, M.A., Meyers, P.M. & McNeley, P.F. 2000. A method to estimate migrant shorebird numbers on the Copper River Delta, Alaska. *J. Field Ornithol.* **71**: 627–637.

Botter, G., Bertuzzo, E. & Rinaldo, A. 2011. Catchment residence and travel time distributions: the master equation. *Geophys. Res. Lett.* **38**: L11403.

Briedis, M., Beran, V., Adamík, P. & Hahn, S. 2020. Integrating light-level geolocation with activity tracking reveals unexpected nocturnal migration patterns of the tawny pipit. *J. Avian Biol.* **51**: e02546.

Crewe, T.L., Taylor, P.D. & Lepage, D. 2015. Modeling systematic change in stopover duration does not improve bias in trends estimated from migration counts. *PLoS One* **10**: e0130137.

Del Villar, J., Garaita, R. & Prieto, A. 2007. *La espátula en la Reserva de la Biosfera de Urdaibai: diez años de seguimiento*. Vitoria-Gasteiz: Servicio Central de Publicaciones del Gobierno Vasco.

Delancey, C.D., Islam, K., Kramer, G.R., MacDonald, G.J., Sharp, A.R. & Connare, B.M. 2020. Geolocators reveal migration routes, stopover sites, and nonbreeding dispersion in a population of cerulean warblers. *Anim. Migr.* **7**: 19–26.

Drever, M.C. & Hrachowitz, M. 2017. Migration as flow: using hydrological concepts to estimate the residence time of migrating birds from the daily counts. *Methods Ecol. Evol.* **8**: 1146–1157.

Farmer, A. & Durbian, F. 2006. Estimating shorebird numbers at migration stopover sites. *Condor* **108**: 792–807.

Fernández-Cruz, M., Alonso, J.A., Garcia-Rúa, A., Pereira, P., Pérez-Chiscano, J.L. & Veiga, J.P. 1981. La migración e invernada de la Grulla Común (*Grus grus*) en España. Resultados del proyecto Grus (Crane Project). *Ardeola* **26**: 1–164.

Flack, A., Aikens, E.O., Kölzsch, A., Nourani, E., Snell, K.R., Fiedler, W., Snell, K.R.S., Linek, N., Bauer, H.G., Thorup, K., Partecke, J., Wikelski, M. & Williams, H.J. 2022. New frontiers in bird migration research. *Curr. Biol.* **32**: R1187–R1199.

Frederiksen, M., Fox, A.D., Madsen, J. & Colhoun, K. 2001. Estimating the total number of birds using a staging site. *J. Wildl. Manag.* **65**: 282–289.

Garaita, R. & Arizaga, J. 2015. The benefits of a constructed lagoon for the conservation of Eurasian spoonbills (*Platalea leucorodia*) in a tidal marsh. *J. Nat. Conserv.* **25**: 35–41.

Horton, K.G., La Sorte, F.A., Sheldon, D., Lin, T.-Y., Winner, K., Bernstein, G., Maji, S., Hochachka, W.M. & Farnsworth, A. 2019a. Phenology of nocturnal avian migration has shifted at the continental scale. *Nat. Clim. Chang.* **10**: 63–68.

Horton, K.G., Van Doren, B.M., La Sorte, F.A., Cohen, E.B., Clipp, H.L., Buler, J.J., Fink, D., Kelly, J.F. & Farnsworth, A. 2019b. Holding steady: little change in intensity or timing of bird migration over the Gulf of Mexico. *Glob. Chang. Biol.* **25**: 1106–1118.

Kaiser, A. 1999. Stopover strategies in birds: a review of methods for estimating stopover length. *Bird Study* **46**: 299–308.

Liechti, F., Bauer, S., Dhanjal-Adams, K.L., Emmenegger, T., Zehtindjiev, P. & Hahn, S. 2018. Miniaturized multi-sensor loggers provide new insight into year-round flight behaviour of small trans-Sahara avian migrants. *Mov. Ecol.* **6**: 1–10.

Linscott, J.A. & Senner, N.R. 2021. Beyond refueling: investigating the diversity of functions of migratory stopover events. *Ornithol. Appl.* **123**: duaa074.

Lok, T., Overdijk, O. & Piersma, T. 2013. Migration tendency delays distributional response to differential survival prospects along a flyway. *Am. Nat.* **181**: 520–531.

Luna, E., Castañeda, C., Gracia, F.J. & Rodríguez-Ochoa, R. 2016. Late Quaternary pedogenesis of lacustrine terraces in Gallocanta Lake, NE Spain. *Catena* **147**: 372–385.

Marion, L. 2013. Recent trends of the breeding population of Spoonbill in France. In Navedo, J.G. (ed) *Proceedings of the Eurosite VII Spoonbill Workshop*: 38–43. Santoña: Eurasian Spoonbill Working Group.

Molina, B., Prieta, J. & Lorenzo, J.A. 2017. Ornithological newsletter (Noticiario Ornitológico). *Ardeola* **64**: 443–478.

Mooser, R. & Woutersen, K. 2015. Common crane migration over the Pyrenees of Huesca – Spain, spring 1980–2015 (Grullas sobre Huesca, primaveras 1980–2015). *Bol. Ornitol. Osc.* **11**: 4–64.

Navedo, J.G. & Garaita, R. 2012. Do systematic daily counts reflect the total number of birds using stopover sites during migration? A test with Eurasian spoonbill. *J. Nat. Conserv.* **20**: 242–246.

Navedo, J.G., Masero, J.A., Overdijk, O., Orizaola, G. & Sánchez-Guzmán, J.M. 2010a. Assessing the role of multiple environmental factors on Eurasian spoonbill departure decisions from stopover sites. *Ardea* **98**: 3–12.

Navedo, J.G., Orizaola, G., Masero, J.A., Overdijk, O. & Sánchez-Guzmán, J.M. 2010b. Long-distance travellers stopover for longer: a case study with spoonbills staying in North Iberia. *J. Ornithol.* **151**: 915–921.

Newton, I. 2004. Population limitation in migrants. *Ibis* **146**: 197–226.

Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *J. Ornithol.* **147**: 146–166.

O'Reilly, K.M. & Wingfield, J.C. 1995. Spring and autumn migration in Arctic shorebirds: same distance, different strategies. *Am. Zool.* **35**: 222–233.

Orellana-Macías, J.M., Bautista, L.M., Merchán, D., Causapé, J. & Alonso, J.C. 2020. Shifts in crane migration phenology associated with climate change in southwestern Europe. *Avian Conserv. Ecol.* **15**: e16.

Piersma, T., De Goeij, P., Bouten, W. & Zuhorn, C. 2021. *Sinagote, the Biography of a Spoonbill*. Barcelona: Lynx Editions.

Prange, H. 2012. Reasons for changes in crane migration patterns along the west-European flyway. In Harris, J. (ed) *2010 International Workshop in Cranes, Agriculture and Climate Change*: 35–48. Muraviovka Park, Russia and Baraboo, Wisconsin, USA: International Crane Foundation.

Prange, H. & Ilyashenko, E.I. 2019. Species review: Eurasian crane (Grus grus). In Mirande, C.M. & Harris, J.T. (eds) *Crane Conservation Strategy*: 397–423. Baraboo: International Crane Foundation.

Rappoldt, C., Kersten, M. & Smit, C. 1985. Errors in large-scale shorebird counts. *Ardea* **73**: 13–24.

Rinaldo, A., Benettin, P., Harman, C.J., Hrachowitz, M., McGuire, K.J., van der Velde, Y., Bertuzzo, E. & Botter, G. 2015. Storage selection functions: a coherent framework for quantifying how catchments store and release water and solutes. *Water Resour. Res.* **51**: 4840–4847.

Román, J.A. 2022. Phenology and distribution of the common crane (*Grus grus*) in Spain: season 2021/2022. In *Annual Report of the Grus-Extremadura: working Group on the Common Crane Grus Grus*: 190. Extremadura.

Román, J.A., Lekuona, J.M., Onrubia, A., Mooser, R. & Woutersen, K. 2016. *Migración e invernada de la Grulla Común, Grus grus*, en España y Marruecos. Temporada 2015/16. (Annual report of the Grus-Extremadura: working Group on the Common crane *Grus grus*): 73. Extremadura.

Roques, S., Henry, P.-Y., Guyot, G., Bargain, B., Cam, E. & Pradel, R. 2021. When to depart from a stopover site? Time since arrival matters more than current weather conditions. *Ornithology* **139**: 1–13.

Schmaljohann, H., Eikenaar, C. & Sapir, N. 2022. Understanding the ecological and evolutionary function of stopover in migrating birds. *Biol. Rev.* **97**: 1231–1252.

Sprenger, M., Stumpp, C., Weiler, M., Aeschbach, W., Allen, S.T., Benettin, P., Dubbert, M., Hartmann, A., Hrachowitz, M., Kirchner, J.W., McDonnell, J.J., Orlowski, N., Penna, D., Pfahl, S., Rinderer, M., Rodriguez, N., Schmidt, M. & Werner, C. 2019. The demographics of water: a review of water ages in the critical zone. *Rev. Geophys.* **57**: 800–834.

Triplet, P., Overdijk, O., Smart, M., Nagy, S., Schneider-Jacoby, M., Karauz, E.S., Pigniczki, C.S., Baha El Din, S., Kralj, J., Sandor, A. & Navedo, J.G. (eds) 2008. *International single species action plan for the conservation of the Eurasian spoonbill Platalea leucorodia*. AEWA Technical Series No 35. Bonn: AEWA.

Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. *J. Avian Biol.* **41**: 621–626.

Weber, T.P., Houston, A.I. & Ens, B.J. 1994. Optimal departure fat loads and stopover site use in avian migration: an analytical model. *Proc. R. Soc. Lond. B Biol. Sci.* **22**: 29–34.

Weisshaupt, N., Lehtiniemi, T. & Koistinen, J. 2021. Combining citizen science and weather radar data to study large-scale bird movements. *Ibis* **163**: 728–736.

Received 24 March 2023;
Revision 16 April 2025;
revision accepted 3 June 2025.
Associate Editor: Phil Battley

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Simulations to test hydrological modelling approach.

Figure S1. Correlation between the number of Common Cranes observed departing Gallocanta and the measures of outflow predicted by the hydrological model in the calibration sample (years 1984 and 1985).

Figure S2. Correlation between the number of Eurasian Spoonbills observed departing from two coastal wetlands in northern Spain and the measures of outflow predicted by the hydrological model.

Table S1. Information sources of modelling migration dynamics of Common Cranes and Eurasian Spoonbills in Spain. Roman numerals add further details at the bottom of the table.