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Dynamic multistate occupancy modeling to evaluate population dynamics under a scenario of preferential sampling

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Abstract. Effective conservation of animal populations depends on the availability of reliable data derived from rigorous monitoring protocols, which allows us to assess trends and understand the processes they are governed by. Nevertheless, population monitoring schemes are hampered by multiple sources of errors resulting from specific logistical and survey constraints. Two common complications are the non-visitation of some sites in certain years and preferential sampling (PS), that is, the tendency to survey "better" sites disproportionately more often. Both factors can lead to serious biases unless accommodated into models. We used 22 yr of nest-monitoring data to develop a dynamic multistate occupancy model, including a PS component to investigate occupancy and reproduction dynamics in a peripheral Black Stork (*Ciconia nigra*) population in Spain. We analyzed the effects of climate and nesting substrate (tree vs. cliff) on population dynamics and accounted for PS and non-visitation biases using a model that distinguished three territorial states: unoccupied, occupied without, or occupied with successful reproduction. We found strong evidence for positive PS, and when accounting for this bias, lower population size estimates were generated. Black stork nests had a high probability of remaining in the same state from one year to the next, with successful nests more likely to be occupied again and to be successful the following year than occupied but unsuccessful or unoccupied nests. Nesting substrate and spring precipitation did not influence state transition probabilities or the probability of reproductive success; nevertheless, cliff nest occupancy was overall higher than tree nest occupancy. Our results highlight the importance of correcting for non-visitation and PS in habitat occupancy models. If these potential biasing effects are not accounted for, inferences of population size may be overestimate. Multistate occupancy models with correction for PS offer a powerful analytical framework for data collected as part of population studies of unmarked animals. These models compensate for common methodological biases in biological surveys and can help implement efficient conservation strategies based on robust population dynamics estimates.

Key words: Bayesian inference; bias sampling; Black Stork; occupancy models; population dynamics; population survey; species distribution.

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Introduction

Increased pressure from human action and global change are driving unprecedented levels of biodiversity loss (Brook et al. 2008, IPBES 2019). There is overwhelming evidence indicating that the extinction risk of a species increases when its population size begins to decline (Norris 2004). However, a more fundamental understanding of the links between population processes and global environmental changes are still required to identify appropriate management and conservation strategies (Ehrlén and Morris 2015). Most biodiversity conservation studies focus on measuring species richness and patterns of species occurrence (Schurr et al. 2012); however, much less attention is paid to understanding the dynamic processes that create these patterns, that is, species' population dynamics (but see Schaub and Abadi 2011, Zipkin et al. 2019). A focus on just changes in species' ranges may fail to capture many of the population-level processes—including local extinctions and recolonizations, and the changes in demographic rates that govern them—that underlie these shifts. Therefore, the implementation of effective conservation measures requires the assessment of population dynamics, while the interpretation of population fluctuations obliges us to undertake specific and long-term monitoring studies (Nichols et al. 2007).

In this study, we used 22 yr of nest-site occupancy data to explore the population dynamics of a peripheral and geographically isolated black stork (*Ciconia nigra*) population in the southwestern extreme of its Palearctic range (W Spain; del Hoyo et al. 1992). The black stork has an unfavorable conservation status in Europe (listed in Annex I of the EU Birds Directive; 2009/147/EC) and has undergone severe population declines in some parts of its Palearctic range (Konovalov et al. 2019). In light of this, inference regarding the dynamics of nest occupancy and breeding success will be of particular interest when designing monitoring and conservation programs and will facilitate long-term evaluations of population dynamics and interannual variations. However, accurately determining population dynamics from long monitoring schemes, as our dataset, is a major challenge, since these programs are difficult to maintain over time and in consequence often suffer from a lack of standardized protocols (Kéry and Schmidt 2008, Johnston et al. 2020). Therefore, incorrect conclusions about monitored populations can arise from different biases (Irvine et al. 2018), such as imperfect observation (Kéry and Schmidt 2008, Kéry and Royle 2016), non-random sampling (Yoccoz et al. 2001), and coverage bias, which occurs when some sites are not visited in certain years (Van Strien et al. 2004, Monneret et al. 2018).

One crucial type of non-random sampling bias appears when survey effort is not randomly allocated over space or time, and (positive) preferential sampling may arise if sites, where species are thought or known to be present, are oversampled (Diggle et al. 2010, Conn et al. 2017, Monneret et al. 2018, Johnston et al. 2020, Kéry and Royle 2021). Neglecting those uncertainties and causes of bias can significantly reduce the reliability of estimates of population dynamics (MacKenzie et al. 2003, Diggle et al. 2010, Guillera-Arroita 2017). In the context of population changes, a powerful emergent approach for overcoming these sampling biases is using dynamic occupancy models. These models can account for imperfect species detection by simultaneously modeling the surveying and occurrence processes that underlie observational data while accommodating environmental and other covariates of interest (MacKenzie et al. 2003, 2009, 2017, Royle and Kéry 2007). Bayesian inference is particularly efficient at coping with missing values in this type of models. Furthermore, extensions of such occupancy models allow us to deal with a number of different states including multiple abundance classes and breeding vs. nonbreeding states (Royle and Link 2005, Nichols et al. 2007, MacKenzie et al. 2009). This greatly increases the applicability of these methods to ecology and conservation and allows us to investigate mechanistic hypotheses beyond species distribution patterns that can be used to explore the processes driving these patterns (McGrady et al. 2017).

Here, we used a dynamic multistate occupancy model together with a multistate extension of the approach developed by Conn et al. (2017) and Monneret et al. (2018) of modeling the selection of data locations jointly with occupancy and productivity to test whether the monitoring scheme was under positive preferential sampling and, if so, assess the black stork population dynamics properly (but with no component for imperfect detection; see methods). It is essential also to consider that the occupancy and breeding performance of black stork populations may be influenced by both extrinsic (e.g., climate) and intrinsic (e.g., previous breeding experience) factors. In Europe, habitat destruction and forest degradation are cited as the main threats to black storks populations (BirdLife 2004, Lõhmus et al. 2005). Although in much of Europe black storks nest mostly in trees (Treinys et al. 2008), some pairs also nest on cliffs (Cano-Alonso 2006); this is the case of Spain, where almost half of the black stork population is cliff nesting (Del Moral 2018). Suitable trees for nesting are scarce, which may have caused a progressive shift from trees to cliffs (Cano-Alonso 2004). However, the long-term effects of nesting on different substrates remain unclear. The Spanish black stork population may also be affected by climatic factors (Cano-Alonso and Tellería 2013) since these storks prey mostly on fish: Food availability mainly depends on water levels of the usually smallish water bodies in which these stork find their prey, which in turn depends on rainfall in this arid Mediterranean region (Chevallier et al. 2010). Therefore, we examined the influence of nest type as a site covariate and the average amount of precipitation during the year as a site-by-year-specific covariate. Overall, correct assessments of population fluctuations are vital for making inferences about how occupancy distributions respond to global change (Kéry and Schmidt 2008, Bruggeman et al. 2016). Our specific goals were (1) to test and account for preferential sampling and non-visitation biases in the estimates of population size in the model, and explore occupancy and reproduction dynamics in black storks; and (2) to determine whether interannual variations in occupancy and reproduction dynamics are related to local climatic conditions or nest type.

METHODS

Study area

Our study area was the province of Salamanca ($12{,}349\ km^2$) in north-west Spain (Fig. 1), which consists largely of a plateau with an average altitude of 823 m a. s. l. surrounded by mountains peaking at 2400 m a. s. l. The relief gives rise to great differences in rainfall, which vary from 1000 mm annually in upland areas to about 400 mm in the aridest parts of the region, chiefly in the plains.

Field methods

Raw survey data were provided by the Territorial Environmental Service of Salamanca, Junta de Castilla y León (Fandos 2020). Since 1986, black stork nest monitoring has been conducted by forest rangers backed up by independent observers, who help complete data collection and processing. Surveys were somewhat irregular until the early 1990s, and so here, we base our analyses on data collected in 98 territories monitored in 1992–2013. Fieldwork was conducted between 1 February and early July; most territories were visited on multiple occasions during each breeding season to confirm occupancy by single birds or pairs, and to count the number of nearly fledged young as a measure of fecundity. A territory was considered reproductively successful if it produced at least one fledgling. All nests were georeferenced.

Unfortunately, in the available data, only the aggregate results of the multiple repeated surveys at sites during a single breeding season were reported as opposed to survey-specific results. Typically, multiple repeated surveys within a defined period are required to estimate territory occupancy independently of detection error (Kéry and Royle 2016). Hence, in our model we ignored the possibility of imperfect detection and so what we define as the “occupancy probability” is in fact the “apparent occupancy probability” (Kéry 2011), that is, the product of the probabilities of occupancy and of detection. Since there were multiple surveys per site and year, and given that the survey protocol was fairly well standardized, we would expect a reasonably high and stable detection probability. Consequently, we here make the assumption that spatial and temporal patterns in apparent occupancy reflect occupancy patterns well but not detection patterns. In addition, we interpret relative population size estimates as if they were absolute abundances, once again assuming that the overall detection probability per site and year is high

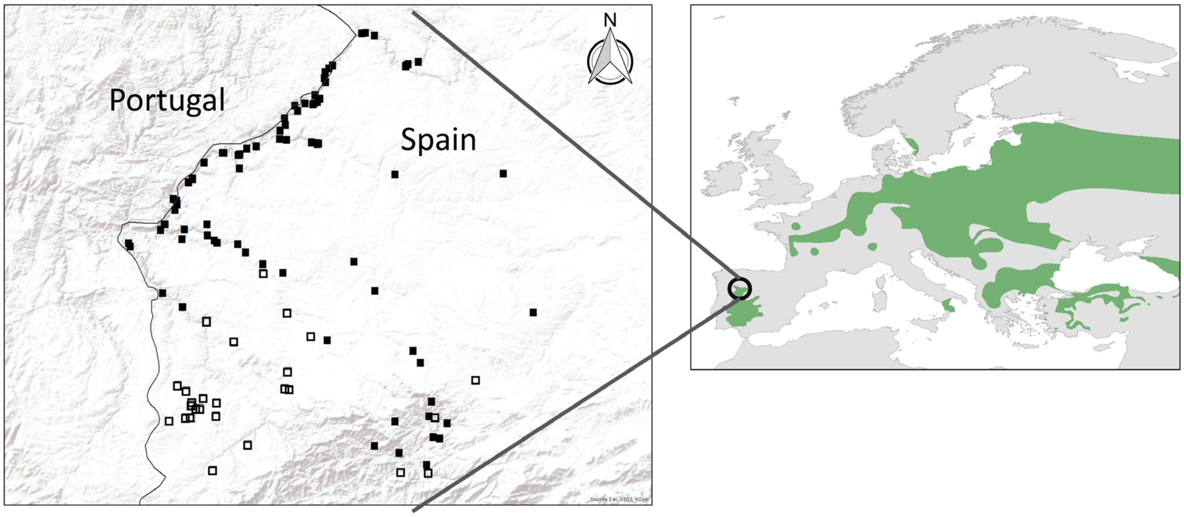

Fig. 1. (Right) European breeding range of the black stork (*Ciconia nigra*) in green (Birdlife 2004). (Left) distribution of the 98 known black stork nests in the study area: Tree nests are shown as open squares and cliff nests as solid squares. A territory was defined as a site with observations of a black stork pair in a suitable nesting structure in at least one year during 1992–2013. It is believed that the vast majority of black stork nesting territories are known.

(see Chapter 1 in Kéry and Royle 2016 and the Introduction to Kéry and Royle 2021).

We calculated the annual mean precipitation totals (mm) for each individual nest location in each year using CHELSA variables (Karger et al. 2017) and scaled them for analysis.

Occupancy modeling

We used Bayesian inference to create a dynamic multistate occupancy model (MacKenzie et al. 2009, Kéry and Royle 2021) that did not include an observation model since we could not estimate the detection probability from the data at our disposal (see Appendix S1). Occupancy models are used to estimate and model the probability of territory occupancy and reproductive success, and to test for the effects of covariates on these parameters. As well, they can be used to obtain annual estimates of population sizes in cases where a "site" can only be occupied by a single pair of birds. This was the case of our study, where a site is equivalent to a territory and can be occupied by either 0 or 1 pair of storks. In addition, we had to tackle two common types of uncertainty or sources of bias in long-term population survey data such as ours (Monneret et al. 2018): the problems of missing values (when there are no visits to a territory in a given year) and of possible preferential sampling. Preferential sampling (PS) is a form of non-random sampling, in which the probability of surveying a territory depends on the probability that the territory is occupied. We would normally expect a positive association, that is, a positive PS (Conn et al. 2017). If not accounted for in an occupancy model, positive PS will lead to an overestimation of the population size and the occupancy probability (Conn et al. 2017, Monneret et al. 2018, Kéry and Royle 2021) and, in addition, may bias perceived population trends (Kéry and Royle 2021).

In our multistate model, we defined three true occupancy states for sites in any particular breeding season: (1) unoccupied—territories that are empty or have only a single bird, (2) occupied without successful reproduction—a pair is present but no successful reproduction takes place, and (3) occupied with successful reproduction—a pair is present and at least one chick fledges. The dynamic part of this model (Appendix S1) ensures that the estimates for any given year will depend on the state of occupation and reproduction in a territory during the previous year (i.e., it accommodates temporal autocorrelation in a dynamical is mechanistic fashion; Wikle et al. 2019) and also allows us to model site-level demographic processes that underlie changes in population size (which in this case is the number of pairs, classified according to their breeding success).

Preferential sampling in avian population studies

In our study, as in many other population studies, territories were not randomly surveyed. Nests that were previously known to have been occupied or were regarded as the most suitable were more likely to be surveyed, while less suitable sites were surveyed less frequently. Hence, it was likely that the surveyed territories represented a sample that was biased toward higher-quality territories. This kind of non-random sampling is known as (positive) preferential sampling (PS; Conn et al. 2017). When PS is not accounted for in models of site-level population dynamics in a population study such as ours, population sizes may be overestimated (Diggle et al. 2010). As well, other estimators may be biased because the values for occupancy and reproduction probabilities for the good territories are extrapolated to the territories that were not visited, which will tend to be of inferior quality and therefore differ in their occupancy and reproduction values.

We accounted for potential preferential sampling by developing a joint model that combines the occupancy submodel with a submodel for the probability that a territory is visited (Conn et al. 2017, Monneret et al. 2018). In this specific joint model, we use whether a site was occupied or not during the previous breeding season, combining the two states occupied without breeding and occupied with reproduction, as a predictor in the logistic regression submodel that describes whether or not a site is visited. In the case of positive preferential sampling, the quality of the site (i.e., whether or not it was occupied at time t) is expected to have a positive effect on the probability of visiting a site at time $t + 1$ (Fig. 2).

Fitting model

We established a dynamic multistate model to allow occupancy and reproduction probabilities to vary over space and time as a function of environmental covariates. In particular, we introduced nest type and precipitation as covariates, and the site as a Gaussian random factor in the occupancy, reproduction, and transition estimation. Besides, we account for preferential sampling by specifying the joint model for occupancy and the visitation probabilities of a site by specifying a dependent correlation structure between the two processes. The visitation of a site depends on whether a site was occupied (regardless of nesting success) during the previous breeding season. Besides, we established three more dynamic multistate occupancy models that differed in complexity, to understand how the model parameters governing state dynamics may or may not be affected by heterogeneous site quality, between-year dynamics, and preferential sampling biases (Appendix S2: Fig. S1).

We fitted all models with Bayesian methods using vague priors in the program JAGS (Plummer 2003) run from R with package jagsUI (Kellner 2016). We ran the chains for long enough to ensure that convergence was reached based on the Brooks-Gelman-Rubin statistic (Gelman and Rubin 1992, Brooks and Giudici 2000). We provide the model code in BUGS language in Appendix S5.

RESULTS

Our dataset included 98 nests that were monitored at least once over the 22-yr study period (1992–2013). In 29 territories, the nest was on a tree, while in 69 it was on a cliff. On average, only 24 territories (i.e., about 24%) of all territories were surveyed in any given year, a percentage that varied annually from 9% to 75% (Fig. 3). In addition, we found strong evidence for the heterogeneous quality of the territory and for positive preferential sampling: Sites that were occupied during the previous year were more likely to be surveyed than sites that had not been occupied the preceding year (Table 1; Fig. 2, Appendix S4).

Given that there was strong evidence for PS in our model (visitation and occupancy probabilities were highly correlated; Fig. 2), it is essential accounting for it to avoid the overestimation of population size. This model (red in Fig. 3)

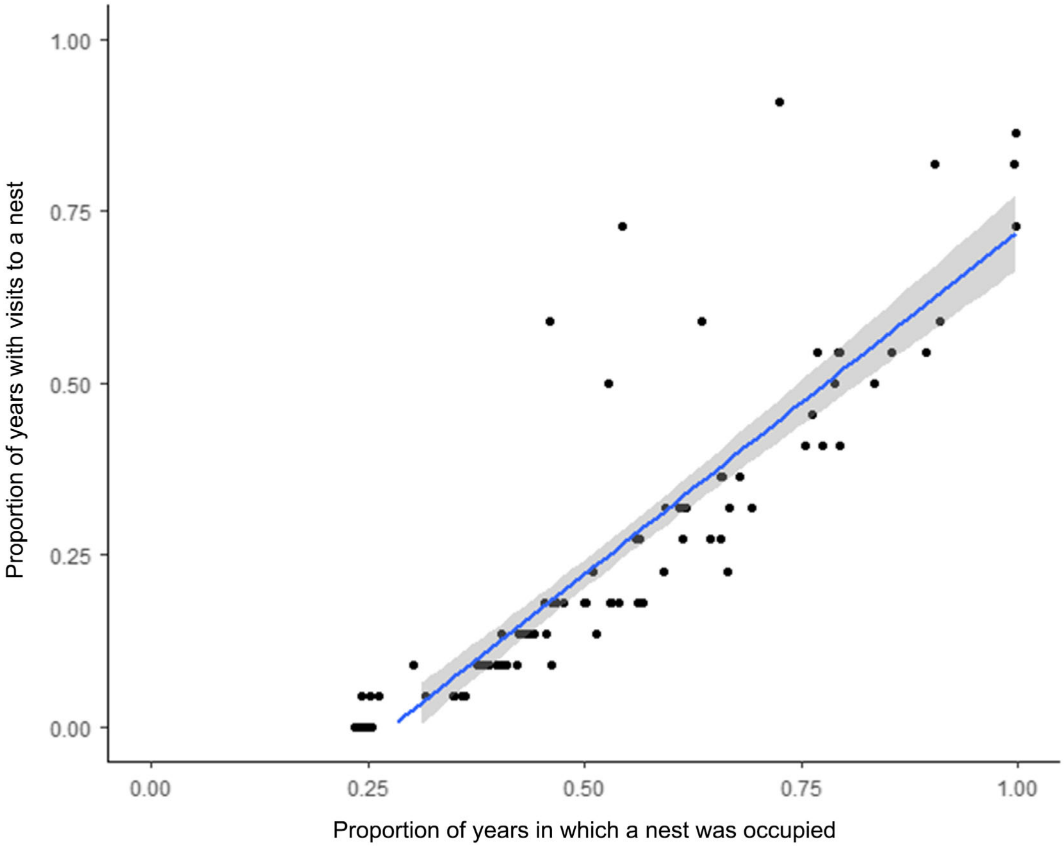

Fig. 2. The evidence for preferential sampling in the Spanish black stork population study: the relationship between the proportion of years in which a territory was visited and the proportion of years (of those in which it was visited) in which a territory was occupied (with or without breeding). The blue line is the linear regression, which explains 78% of the variance ($F = 345.2$, df = 96, $P < 0.001$).

indicates that the probability of occupancy and reproduction fluctuated in a similar fashion over the years, although the proportion of territories with reproduction was higher in all years than the proportion of territories occupied without reproduction (Appendix S3: Fig. S1). Under this model, and under the assumption that the effective detection probability in any given year was close to one, the population size was very dynamic during the study period: The number of pairs declined between 1992 and around 2003 from ~60 to ~20 pairs but then rapidly increased to 60–80 pairs. The estimates of the number of territories with successful breeding (nests in which ≥1 fledged chick) ranged from 44.8 ± 8.8 in 1992 to 43.6 ± 10.6 in 2013, with a maximum of 60.8 ± 13.1 in 2005 and a minimum of 11.4 ± 4.4 in 2003 (Fig. 3). On the other hand, the estimates of the number of occupied territories without reproduction varied from 11.8 ± 6.6 in 1992 to 27.4 ± 7.6 in 2013 (maximum), with the minimum in 1997 with 7.7 ± 2.8. The trends of both occupancy and reproduction probabilities followed similar patterns in both nest types (Appendix S3: Fig. S1). However, the occupancy probability was higher in cliff- than tree-nesting territories (Table 2). By contrast, the reproduction probability did not vary between nest types (Table 2).

There were few dynamics in the state transition matrix (Table 1) as most territories remained in the state they were in from one year to the next. These transition probabilities did not vary according to the type of nesting substrate

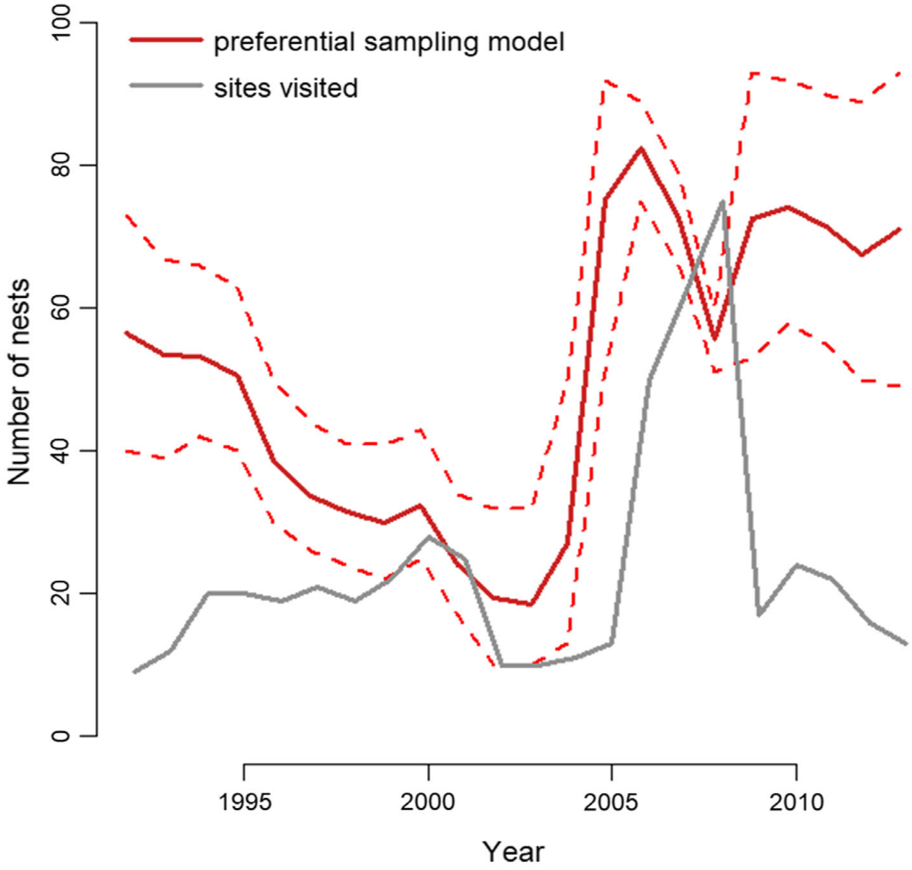

Fig. 3. Number of visited nests, and the estimated population sizes (number of occupied territories; with and without reproduction) with 95% Bayesian credible intervals (dashed red line) for Spanish black storks under the dynamic multistate occupancy models with preferential sampling for 1992–2013.

Table 1. Posterior means and standard deviations of the probabilities in the transition matrix for the studied black stork population under a dynamic occupancy model with preferential sampling.

State	Unoccupied	Occupied	Successful
Unoccupied	0.802 ± 0.038	0.090 ± 0.025	0.108 ± 0.027
Occupied	0.272 ± 0.052	0.384 ± 0.046	0.344 ± 0.049
Successful	0.108 ± 0.023	0.240 ± 0.028	0.653 ± 0.030

Notes: Rows indicate the state in year t and columns the state in year $t + 1$. Hence, the diagonal cells represent the probability of staying in the same state, and the off-diagonals represent the probability of changing from one state to another state.

(transition probability; Appendix S3: Table S1). However, occupancy and reproduction varied strongly over time since the year had an effect on both estimates (Table 2).

DISCUSSION

Monitoring territory occupancy has proved useful for assessing the population trends of many animal species and enables us to determine their conservation status and evaluate the efficiency of conservation plans (Ficetola et al. 2018). Here, the application of a dynamic multistate site occupancy model (MacKenzie et al. 2009) to 22 yr of nest-monitoring data from a peripheral black stork population in Spain allowed us to jointly estimate occupancy and reproduction success dynamics while accounting for two important mechanisms of observation bias: non-visitation and preferential sampling. Addressing these two types of bias was crucial because we avoid an overestimation of this stork's long-term population dynamics due to, firstly, incomplete

Table 2. Posterior probability summaries of parameters evaluated in the black stork dynamic occupancy model with preferential sampling.

Parameter	Mean	SD	95% credible interval
Initial occupancy probability			
beta.lpsi[tree]	−0.326	3.029	−6.297, 5.563
beta.lpsi[cliff]	4.003	1.769	0.768, 7.785
Initial reproduction probability			
beta.lr[tree]	−1.026	3.03	−7.092, 4.929
beta.lr[cliff]	−0.115	2.345	−4.737, 4.5
Coefficient for preferential sampling			
beta.theta	5.119	0.440	4.278, 6.005

survey coverage (i.e., a non-visitation bias since the number of surveyed territories varied over time) and, secondly, positive preferential sampling (successful nests were more frequently visited than others). These methodological challenges are commonplace in monitoring surveys of territorial species, and so we decided to explore the ability of occupancy models to reduce the effect of these types of bias (MacKenzie et al. 2003, 2017, Monneret et al. 2018, Kéry and Royle 2021). This framework can be employed as a guide for developing more robust estimates using data from long-term surveys of unmarked animals showing high interannual variability due to logistical and survey conditions that change over time. Likewise, this methodology will provide a better understanding of the different population processes that are essential for the conservation and management of wildlife species (Jones et al. 2016).

Our study of the black stork in the Iberian Peninsula revealed that occupancy and reproduction dynamics followed a similar trend over time. This population reached minimum levels in 2003, with an estimated 18 adult pairs, of which we believe that 11 bred. The model suggest a very considerable increase in territory occupancy and reproduction after 2005 (Fig. 3). Although we corrected for overestimation caused by the positive preferential sampling, this sharp increase in the population size could be an artifact of the high sampling effort conducted during specific years, in which many new territories were sampled for the first time or due to a systematic temporal pattern in detection probability, that we were unable to account for in our analysis. (Fig. 3). Transition probabilities between different states show that, compared with nests that were unoccupied or occupied without breeding in the previous year, there was a substantially higher probability of a nest being occupied or occupied with successful reproduction if fledglings were produced during the previous year. The high probability of remaining in the same state the following year could indicate that the quality of the site and/or the quality of breeding pairs are important in determining population size and reproduction state over time (Lee and Bond 2015). This result supports the hypothesis that some nests were more valuable than others (Lee and Bond 2015) because they made disproportionately greater contributions to the overall population size (Runge et al. 2006). Additionally, nest-site fidelity, an adaptive strategy in Ciconiiformes (Cézilly et al. 2000), is highly correlated to the breeding success in the previous season (León-Ortega et al. 2017). However, our inferences cannot be extended to individual black storks directly because we worked with unmarked individuals. Hence, the "unit" in our study was the occupied nest, not the individual bird. Therefore, we were unable to demonstrate whether or not successful nests (in terms of occupancy or reproduction) were influenced by the habitat quality around the nest and/or whether or not individuals with high reproductive abilities (e.g., previous breeding experience) occupied these better areas. In practice, the two are likely to be correlated, with better individuals occupying better sites (Wilson et al. 2018).

The occupancy and reproduction dynamics in cliff-nesting and tree-nesting pairs were similar. Our finding that the occupancy probability for cliff nests was higher than for trees (Table 2) can be interpreted as a lack of suitable forests for nesting (Ferrero and Román 1991, Tamás 2012). However, we found no association between the reproduction probability and nesting substrate. This result agrees with previous studies of black stork nest productivity (mean number of fledged chicks/nest) that have found no significant differences between nesting substrates in subpopulations (Cano-Alonso and Tellería 2013). When pooled, results from both nesting substrates reflect the ecological variability of the species in this area and indicate the plasticity of the species and its ability to adapt its nesting behavior to the available habitat. The other covariate included in our analysis, precipitation, did not have a substantial impact on either occupancy or reproduction. Most of the nests occurred within a range of typical precipitation values, although a broader range of precipitation would probably have a more significant effect on black stork population dynamics. The explicit incorporation of other factors into our model that might influence occupancy and reproduction (e.g., the presence of cliff-nesting raptors or the availability of food resources) could become an important line for future research. Since the black stork is listed as Vulnerable in Spain, the species requires strict protection and regular monitoring of its population for use in recovery or conservation plans. We believe that this study, based on 98 nests monitored over 22 yr, is one of the longest-running surveys of population size and reproduction dynamics of any black stork population worldwide. Our results highlight the vital role played by successful nests to this population of black storks, which are more likely to occupy sites if the nest was successful the year before. This information could help managers identify and take appropriate conservation measures in the areas that make disproportionately large contributions to this stork's population productivity and persistence.

One important caveat for interpreting our results is that we did not bear in mind the possible imperfect detection of occupied sites. Although most nests were visited many times during the breeding season, we had no information about how observations took place at occupied and successful nests because our database generally only included the aggregated survey results for each territory and year. We believe that imperfect detection might affect our results and lead to an underestimation of the probability of nest occupancy and successful reproduction events and thus, in turn, to the underestimating of population sizes, which may hinder attempts to detect stronger covariate effects (Gu and Swihart 2004). The long time scale of the monitoring program, as well as its great spatial coverage, leads inevitably to high temporal heterogeneity in the proportion of nests visited each year. This great variability could bias estimates of population dynamics, especially at the beginning of the study period, when the sampling effort was deficient (Fig. 3). Additionally, novel technologies such as camera traps show that black storks may have more than one nest in a single territory (Cano-Alonso and Sundar 2018, Cano-Alonso et al. 2019). Therefore, although our estimates might not be straightforwardly interpreted into population size, these estimates will not give biased estimates of trends in occupancy and reproduction (unless there were trends in detection probability over time). Clearly, for future analysis, visit-specific detection data will necessary to be able to correct the model for imperfect detection. However, we feel that it is worth emphasizing that the power of dynamic occupancy models can be used without an observation model and to derive valuable insights into population dynamics in a study of unmarked animals.

In the context of conservation, where severe funding limitations are habitual (Martin et al. 2018), occupancy modeling is a valuable tool for monitoring populations in a wide variety of contexts and for accounting for many of the methodological biases common in biological surveys (MacKenzie et al. 2017). In this case, we corrected our estimates to avoid the effects of incomplete survey coverage and positive preferential sampling (Monneret et al. 2018). However, our dynamic multistate occupancy approach could be easily extended to model the impact of different covariates and to estimate the probability of detection when data regarding the observation process is available (MacKenzie et al. 2009). We suggest that in bird population monitoring programs, it is vital to continue surveys after the first detection at a territory and to record in databases the results of every visit. This temporal replication is required for estimating detection probabilities and therefore for rigorously correcting for non-detection biases. Repeated surveys need not necessarily be performed for all territories since there are always trade-offs between the number of sites sampled and the sampling effort undertaken per site. It would be sufficient to record these additional survey results individually for a selection of territories (Bailey et al. 2014). Statistical approaches, nevertheless, only partially address these methodological biases (MacKenzie and Royle 2005). Improvements in survey designs and the standardization of sampling protocols (e.g., random or systematic sampling) will allow wildlife managers to implement conservation strategies based on robust population models that will increase the resilience of populations under a scenario of rapid global change (Jones et al. 2016).

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DATA AVAILABILITY

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3469/full