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Forum

Estimating nest-switching in free-ranging wild birds: an assessment of the most common methodologies, illustrated in the White Stork (*Ciconia ciconia*)

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Reliable estimates of nest-switching are required to study avian mating systems and manage wild populations, yet different estimation methods have rarely been integrated or assessed. Through a literature review and case study, we reveal that three common methods for assessing nest-switching blend different components, producing a wide range of estimates. Careful component definition and reporting are essential to properly estimate this behaviour.

Keywords: breeding dispersal, genetic kinship analysis, GPS tracking, multi-method comparison, nest fidelity, ring resighting, standardized methodologies.

Nest-switching, displacement from a previous breeding site to a new site (formally defined in Box 1), typically occurs when breeding success is low, birds are inexperienced or competition is high. Contrarily, nest fidelity is common in successful breeders and monogamous species (Greenwood 1980, Shields 1984). Lower levels of switching are associated with increased parental care, reduced conflict with neighbours, effective movement and improved resource utilization, even if conserved territories are sub-optimal (Vergara *et al.* 2006, Culina *et al.* 2015). Therefore, nest-switching can determine breeding success (Greenwood & Harvey 1982, Collias & Collias 2016). Despite their importance, methods for estimating nest-switching in free-ranging birds are not standardized, making cross-study comparison difficult.

Nest-switching is often discussed in relation to breeding dispersal, the distance between successive breeding sites. A dispersal distance of zero represents fidelity; non-zero distances can be categorized as local, regional or long-distance (Box 1). Most reports of avian dispersal are local and regional (Greenwood & Harvey 1982, Paradis *et al.* 1998, Hansson *et al.* 2002, but see Dale *et al.* 2006) but it is unclear whether these reports represent species breeding ecology or methodological constraints.

Here we review recent studies of nest-switching from a methodological perspective and analyse sensitivity of switching estimates to different data collection and processing methods using the White Stork *Ciconia ciconia* as a case study.

LITERATURE REVIEW

We reviewed 89 recently published or highly cited nest-switching and breeding dispersal studies (list of papers and inclusion criteria in Appendix S1). After selection, the sampling method was determined; in some cases, multiple methods were employed. Most (82 of 89) studies assessed switching based on direct nest monitoring or ring recovery/resighting data ('ringing'). Direct observation is optimal for species with

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Box 1: Definitions of true and confounding components of nest-switching behaviour with examples from the presented case study

Breeding site. *Definition:* The site used for breeding – a physical place (e.g. nest, burrow), territory or other pre-defined area. *Case study:* The location of the nest.

(Nest)-switching. *Definition:* Any displacement from a previous breeding site to a new site in the following breeding attempt or breeding season (unit of time explicitly defined). *Case Study:* Displacement from the nest used in the previous breeding season.

Fidelity (*F*). *Definition:* The absence of switching; birds breeding in the same breeding site for two consecutive years (or other unit of time). *Case study:* Cases in which storks bred in the same nest for two consecutive years. These cases can be identified from tagging and genetic data. From our ringing data, *F* cannot be differentiated from very short-range switches (*L*, below) due to poor spatial resolution of data.

Breeding dispersal. *Definition:* The measure of displacement between the previous breeding site and the current breeding site. This can be zero, continuous or discrete. *Case study:* Breeding dispersal is measured continuously (the shortest distance between the previous and current breeding site) and also partitioned into three discrete categories – local, regional and long-distance – defined below.

Local switches (*L*). *Definition:* Nest-switching in close proximity (explicitly defined) to the breeding site, e.g. use of a different nest within the breeding territory or use of a neighbouring territory or breeding site. *Case study:* Nest-switches within 2 km of the previous breeding site. These switches represent local switches within villages (storks typically nest on roofs in our study site). They cannot be resolved from our ringing data (spatial resolution too coarse, grouped with *F*) or from our genetic data (only an individual's presence or absence in the focal breeding site in consecutive years is known). They can be determined from the GPS data.

Regional switches (*R*). *Definition:* Nest-switches within the population's breeding range but with dispersal distances greater than those defined for *L*. *Case study:* Nest-switches beyond 2 km from the focal nests but within the study search area (here, ~52 000 km^2), assumed to represent a continuous population based on gene-flow patterns. These switches can be resolved from ringing and GPS data but not from our genetic data.

Long-distance dispersal switches (*LDD*). *Definition:* Nest-switches beyond the breeding range, e.g. emigration. They can be determined from GPS data downloaded over a cellular network/satellites or from ring resightings outside the breeding range. Study sites with buffer zones beyond the range edges may be used to identify some LDD and these types of switches could then be partitioned to LDD-within-buffer or LDD-beyond-buffer. *Case study:* Nest-switches beyond the study area. These switches cannot be directly quantified from any of our data and are included in the *M* component defined below.

Missing birds (*M*). *Definition:* Birds that were not observed (i.e. not resighted, downloaded, sampled) in the second of two consecutive sampling years. This can be due to *LDD*, mortality, tag malfunction or other errors. *Case study:* These cases can be resolved from ringing and tagging data. For our genetic data, cases can be defined as either *F* or as all other options ($L + R + M + P$, below).

Non-nesting storks (*P*). *Definition:* Individuals not breeding in the second of two consecutive years (breeding pause; Shaw & Levin 2013) but present in the breeding range. *Case study:* These cases can be explicitly identified for tagged birds not a part of the *M* category, as data download was accompanied by detailed breeding behaviour observations. For our ringing data, records of $F + B$, *R* and *M* probably include some cases of *P*. Similarly, *P* cannot be independently resolved for any of the non-*F* classifications from our genetic data.

limited breeding dispersal and easily monitored breeding and when researchers are dedicated to long-term studies. Sometimes, though, assessing nest-switching is a secondary goal, and general datasets, like those from ringers, are employed ($n > 20$ reviewed studies, conservative estimate due to ambiguity in some studies; e.g. Naves *et al.* 2006, Caballero *et al.* 2016, Acker *et al.* 2017, Riding & Belthoff 2018, Spendelow & Eichenwald 2018). Use of historical records is inexpensive but records may suffer from underreporting and

non-uniform observation efforts (Greenwood & Harvey 1982, Schwarz & Seber 1999). Furthermore, breeding status is often lacking, though imperfect data may be improved with modelling (e.g. White & Burnham 1999, Sandercock 2006, McClintock & White 2012, Rushing *et al.* 2017, Weiser *et al.* 2018, Ayers *et al.* 2019). Additionally, data processing, specifically regarding missing or non-breeding individuals, and technical errors (e.g. low-resolution location data, misread rings) might skew findings.

More recently, genetic methods have been employed to assess switching (n = 10; e.g. Stow & Sunnucks 2004, Hoffman *et al.* 2006, Bulut *et al.* 2016, Caballero *et al.* 2016). Many nests can be sampled non-invasively or with minimal trapping effort, but genetic analyses can be expensive and, without extensive sampling, breeding dispersal cannot be elucidated (Fowler 2005).

A third method is long-term movement tracking (n = 4; e.g. Badyaev & Faust 1996, Garcia-Heras *et al.* 2019). Movement data, though, are limited to trapped and subsequently tagged birds, and breeding status is often unknown. Furthermore, application of movement studies is limited to larger species, can be cost-prohibitive, and may negatively affect fitness and behaviour (Lameris & Kleyheeg 2017, Severson *et al.* 2019). Finally, it can be difficult to reliably differentiate between missing, dead or dispersed birds; thus, the occurrence of local dispersal may be overestimated. Seven studies reviewed used multiple methods. In some cases, estimates overlapped (e.g. Saunders *et al.* 2018, Li *et al.* 2019); in others, they did not match (Robinson & Jones 2014), were not compared (e.g. Carey *et al.* 1992) or were used to estimate different parameters (e.g. dispersal vs. genetic structure; Botero-Delgadillo *et al.* 2017).

Following data collection, researchers must process missing birds – those not observed in subsequent seasons – and those that take a breeding pause (Shaw & Levin 2013). When missing birds are included in switching estimates, they can be classified as switches (Blackmer *et al.* 2004, Ponnikas *et al.* 2017, Sumasgutner *et al.* 2019) or as some catch-all 'other' category (e.g. Jenkins & Jackman 1993, Garcia-Heras *et al.* 2019). The former inflates switching and the latter underestimates it by ignoring long-distance switches. In many studies, missing birds are ignored, making samples a biased representation of the population with 100% survival and 0% long-distance dispersal (LDD; Cilimburg *et al.* 2002, Baker *et al.* 2017). Thus, some researchers estimate a 'rate of return', with a denominator of all individuals observed in the previous year, and then a fidelity rate as a proportion of returned individuals (e.g. Gauthier 1990, Williams & Rodwell 1992, Bourgeois *et al.* 2014, Hedlund *et al.* 2017, Becker *et al.* 2018). Some researchers further divide the return rate into its components, modelling survival, emigration, immigration and other parameters (e.g. Sandercock *et al.* 2000, Cilimburg *et al.* 2002, Tolvanen *et al.* 2017, Becker *et al.* 2018, Weiser *et al.* 2018). Many other studies of switching, fidelity and breeding dispersal, particularly those examining underlying drivers and implications, only employ the second estimate (e.g. Hoover 2003, Robert *et al.* 2014, Jablonszky *et al.* 2020). In some, it is difficult to ascertain how missing birds were handled.

Ambiguity also surrounds non-breeding individuals, observed either as non-breeders or in non-consecutive years (breeding pause). Non-breeders have been handled as breeders (Payne & Payne 1993, Robert *et al.* 2015, Jenkins *et al.* 2019) or as non-breeders (Williams & Rodwell 1992, Spendelow & Eichenwald 2018), or have been excluded explicitly (Blums *et al.* 2002, Ayers *et al.* 2019) or implicitly (e.g. when only individuals trapped at nests in consecutive years are studied; Part & Gustafsson 1989, Forero *et al.* 1999, Serrano *et al.* 2001, Hervey *et al.* 2019, Ilan *et al.* 2019). Often these decisions must be extrapolated (Danchin *et al.* 1998, Tolvanen *et al.* 2017, Sumasgutner *et al.* 2019).

CASE STUDY: NEST-SWITCHING IN THE WHITE STORK

To demonstrate sensitivity of nest-switching estimates to data collection methods and filtering, we present a case study of nest-switching in the White Stork using three data collection methods and two filtration criteria.

The White Stork is a long-distance migrant known for its social monogamy (Cramp 1978). Ringing studies suggest they are faithful to mate and nest-site (Barbraud *et al.* 1999, Vergara *et al.* 2006, Itonaga *et al.* 2011), but genetic methods have revealed extra-pair paternity (EPP; Turjeman *et al.* 2016). This large bird is suitable for estimating nest-switching because it is easily observed, extensively ringed and tagged, and genetic material from young is easily collected.

We collated data from several independent research bodies and projects in north-eastern Germany, choosing sites and years that would ensure high spatiotemporal overlap across methods (Fig. 1). An umbrella project encompassed studies of migration (GPS; Flack *et al.* 2016, Rotics *et al.* 2016, 2017, 2018, 2021, Zurell *et al.* 2018) and EPP (genetics; Turjeman *et al.* 2016). To increase overlap between GPS and genetic datasets, we expanded sampling beyond the study's initial scope. Ringing data were collated retroactively, thus accurately approximating datasets used in many mating studies.

Sample collection, filtering and switching estimation

We obtained ringing data from the Hiddensee Bird Ringing Centre, Germany (2011–2016, Fig. 1). Juveniles are ringed annually; however, ringing data for adults may only be resolved at the village level (exact nest

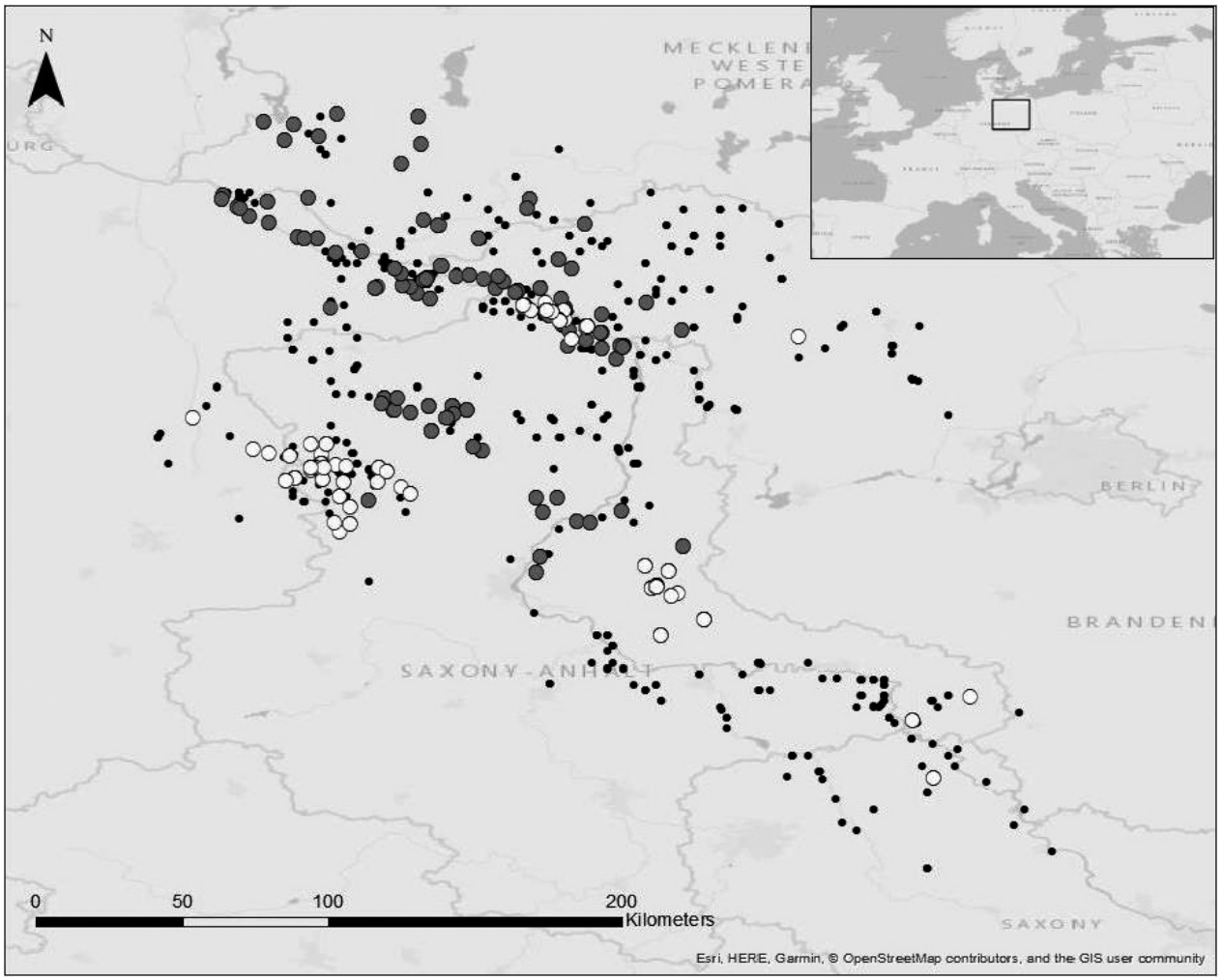

Figure 1. Geographical range for each of the three study methods. This map shows the points of data collection for each of the three study methods. Black dots represent ring resightings (2011–2016); points are thought to be within 2 km of the ringed individual's nesting site. Grey circles represent nests sampled for genetic analysis (2012, 2013, 2015, 2016) and white circles represent nesting locations of GPS-tagged Storks (2011–2015).

coordinates not registered). Two datasets were created to demonstrate how missing individuals affect switching estimates. See Appendix S2 for specific criteria. Briefly, Ring1 (n = 1112) included birds observed in at least the first of two consecutive years (missing birds included), and Ring2 (n = 839) included only birds with recorded resightings in two consecutive years (missing birds excluded). If consecutive recorded locations were within 2 km of one another, no switch was registered. We used this buffer because exact bird locations were unavailable. Birds recorded beyond the buffer, and cases where birds were not observed in the second of two years (Ring1), were denoted switches.

We collected DNA samples (plucked feathers) from White Stork nestlings prior to fledging in 2012, 2013, 2015 and 2016 in north-east Germany (Fig. 1). We performed DNA extractions and molecular work for nests with samples from two consecutive years (696 individual: 126 independent nests plus 19 with samples from all years). Details of sample filtering are given in Appendix S2; methods for DNA extraction, and genotyping are from Turjeman *et al.* (2016; see also Appendix S2). Due to difficulty in trapping adults, we used kinship relatedness analysis without parental genetic material (Blouin 2003), assigning pairs of nestlings from the same nest to three relationship classes and classifying nests as: (1) only full siblings (FS), (2) one or more half siblings (HS), (3) one or more unrelated individuals (U) using the two-programme congruency method from Turjeman *et al.* (2016). We did this within

a single year (to identify EPP) and then over consecutive years, inferring nest-switching of neither, one, or both parents by comparing sibling relatedness in the same nest over two consecutive years. Nestlings identified as HS or U were associated with one or two parent switches, respectively. Complex cases, including incidents of EPP, are addressed in Appendix S2, Figures S1 and S2, and Table S2.

We tagged 62 adult Storks from 2011 to 2013 (see Rotics *et al.* 2016) in an area largely overlapping with the other sampling regions (Fig. 1) and downloaded data in the area through 2016 (no remote download capabilities). Nests were assigned to sites with the highest density of GPS fixes (Rotics *et al.* 2018) and breeding status was confirmed by observation. In the few cases ($n = 4$) where both adults in the nest were tagged, we included only one bird. As with ringing, we built two datasets (Appendix S2). Tag1 ($n = 107$) included all birds that bred in the first of two consecutive years (missing birds included), and Tag2 ($n = 87$) included all Storks found in two consecutive years, as long as they bred in the first year (missing Storks excluded). Storks that returned to the same nest (GPS location) in consecutive years were not switches, regardless of mating status. Storks found at different locations or missing (Tag1) were switches, as were those found but not associated with a nest (breeding pause).

Comparison of switching estimates

For ringed and GPS-tagged individuals, we quantified nest-switching as presence (1) or absence (0) of switching in consecutive years. For genetically tested nests, we quantified switching as no, one or two switches (per nest) based on multi-year relatedness. Males and females were handled together. We made pairwise comparisons of switching estimates, converting genetic comparisons into binary (0/1) switching categories and including only one individual per nest. For each of the datasets, all 2-year comparisons, regardless of year, were grouped and included. We only compared Ring1 with Tag1, Ring2 with Tag2, and the genetic method with all other datasets. We did not compare Ring1 with Ring 2 or Tag1 with Tag 2 as these datasets are nested.

Raw nest-switching estimates ranged from 0.11 to 0.37, and the datasets gave significantly different estimates (Fig. 2, Table 1; Tables S4 and S5). In the three cases with both genetic and movement data for the same Stork, findings were congruent.

Discussion

We quantified nest-switching in >1300 paired nesting incidents using different data collection and filtration methods, with data collated to maximize spatiotemporal overlap. Raw estimates from the datasets varied across methods and between filtration criteria. Ring1 and Tag1 (missing individuals included as switches) probably overestimated switching; modelling is needed to partition missing individuals into categories such as 'switched',

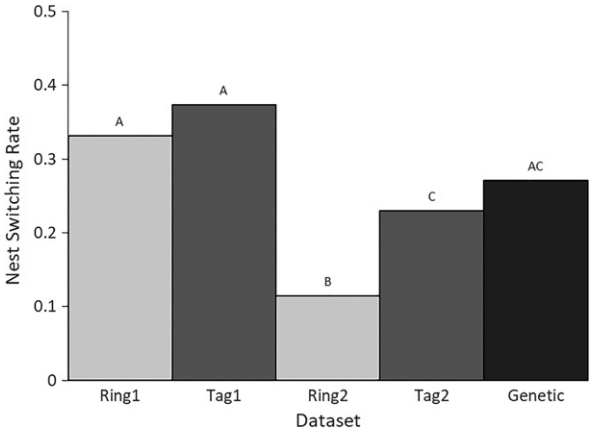

Figure 2. Nest-switching estimates for all employed methods. The rate of switching is presented for two datasets each of ringing and tagging data: individuals that were recorded in at least 1 of 2 years (Ring1/Tag1 – missing individuals included) and individuals recorded in both years (Ring2/Tag2 – missing individuals excluded). Genetic data presented are from 2-year comparisons, reduced to one individual per nest (chosen randomly). Bars marked with the same letter are not significantly different from one another, based on a set of Fisher exact tests with a Bonferroni correction (corrected $\alpha = 00083$).

Table 1. Nest-switching based on ringing, genetic and GPS data.

	Number of switches				
Comparison	0	1	2	Switch rate	*n*
Ring1	743	369	–	0.3318	1112 (408)
Ring2	743	96	–	0.1144	839 (408)
Genetics	55	30	11	0.2708	96
Tag1	67	40	–	0.3738	107 (51)
Tag2	67	20	–	0.2299	87 (39)

For ringed and GPS-tagged individuals, nest-switching events were quantified as presence (1) or absence (0) for two subsets of the data: Ring1/Tag1 (including missing individuals) and Ring2/Tag2 (excluding missing individuals). For genetically analysed birds, nest-switching events were identified as 0, 1 or 2 switches per nest. *n* is the number of 2-year comparisons examined per category. Numbers in parentheses are the number of unique individuals per category in cases where data from more than one 2-year comparison are included. Note that when including only one individual at random from each of the genetic nests, 26 individuals (of 96) switch nests (rate = 0.2708).

'dead' and 'pause'. Removing missing individuals (Ring2, Tag2) probably underestimated switching because some missing individuals may have made long-distance switches. Estimates were consistently lower for ringing than for tagging because we could not resolve local switches from available records. The threshold of <2 km, which approximates data resolution, also resembles the scale of local nest aggregations in East German villages. Switching in the genetic dataset, which includes missing individuals (i.e. not sampled when the same nest is resampled), was slightly lower than in the Ring1 and Tag1 estimates. We excluded nests without genetic samples in the second year, some of which probably represented switches. The difference between Ring2 and Tag2 is surprising, as local switches missing in Ring2 cannot close this gap. Assuming all resighted birds were breeders could have depressed the Ring2 switching rate in comparison with movement-based methods in which breeders were differentiated from non-breeders (classified as switches). Findings in the context of previous White Stork research are given in Appendix S2.

SYNTHESIS TOWARDS BETTER RESEARCH PRACTICES

Before addressing how to assess nest-switching in free-ranging animals, it is important to understand what this behaviour comprises. In Box 1, we define the various components of switching, giving examples from our case study. Benefits and limitations of the various methods are summarized in Table 2.

Different studies have different aims. For some, the main aim is to quantify nest-switching or fidelity. As such, it is important to use a common denominator representing the entire breeding population (e.g. all sampled birds, as in return-rate calculations). Within this denominator, proportions of fidelity and switching will not sum to 1 because missing birds and non-breeders also exist. These birds should be classified as 'other' or, ideally, through modelling, partitioned into subcategories (e.g. pause, temporary or permanent LDD, death; for examples, see Becker *et al.* 2018, Ayers *et al.* 2019). Researchers must also clarify (1) whether only one potential switching event (i.e. one 2-year

Table 2. Methods employed to assess nest-switching.

Method	Filtration options	Strengths	Limitations	Improvements
Ringing	Found in at least one of two consecutive years Found in two consecutive years	Inexpensive, large proportion of population easily tracked, long-term data can be obtained retroactively	Must trap individual, must re-sight or re-trap, difficulty in determining dispersal vs. mortality, additional observations needed to determine breeding status, poor location resolution, prone to observation bias	Study specific data collection rather than retroactive collation, inclusion of a search buffer beyond the focal population's breeding range
GPS tagging	Data in at least one of two consecutive years Data in two consecutive years	High-resolution movement data without observation effort, track multiple years, remote data download can help differentiate dispersal from death	Expensive, must trap individual, difficulty in determining dispersal vs. mortality if remote data download is unfeasible, additional observations may be needed to verify breeding status and mortality rate, limited to relatively large-bodied species, tag lifetime can limit extent of long-term tracking	Lighter tags enable tagging a wider variety of species, less expensive tags enable tracking a larger proportion of the population, remote data download reduces observer biases
Genetic testing	Adult feathers retrieved in at least one of two consecutive years Adult feathers retrieved in two consecutive years Two-year nest-wide offspring comparisons	Sample non-invasively/only offspring, uncover EPP, breeding output data for many mating pairs	Need for dedicated lab space and expertise, individual identity remains elusive without high-resolution, species-specific markers, no measure of dispersal distance or mortality, some methods are expensive	Costs of whole genome sequencing and genotyping by sequencing are decreasing, improved kinship assignment allows application in non-model species

Strengths and limitations of the various methods employed to estimate nest-switching in free-ranging birds along with potential or recently implemented improvements.

observation) is included (reduced data dependencies), (2) whether males and females are treated separately (sexually dimorphic breeding behaviour) and, if not, (3) whether one or both individuals per nest are included (we do not recommend this: behaviours are probably not independent).

Other studies examine drivers and implications of switching. We believe it is important to include missing birds and non-breeders (as above) and to assess drivers of breeding pause and long-distance dispersal in addition to mechanisms driving local and regional breeding dispersal. Yet challenges have led many researchers to address mechanistic questions regarding switching behaviour using a subset of their data – the birds that returned/nested in two consecutive years (see literature review). In these cases, it is important for researchers to discuss their findings in light of potential biases that arise from the exclusion of missing and non-breeding birds. While it seems trivial to dedicate text explaining how switching was measured, including this discussion allows readers to understand and accurately interpret findings, enabling cross-study comparisons and syntheses.

Because avian studies of nest-switching and breeding dispersal (distance) have generally been based on direct observations data, most dispersal events are thought to be local or regional (Greenwood & Harvey 1982, Paradis *et al.* 1998), in line with resighting efforts. We suggest researchers include an additional 'searching buffer' beyond their focal site (e.g. Ponchon *et al.* 2018) to increase detection of longer-distance switches. Until recently, tagging studies faced a similar bias (Strickland *et al.* 2011), which remote data transfer and acceleration logging have reduced by uncovering LDD and mortality events (Garcia-Heras *et al.* 2019, Sergio *et al.* 2019, Rotics *et al.* 2021). Genetic studies based only on offspring give reasonable estimates of switching, but parental death cannot be differentiated nor dispersal distance deciphered. Shed adult feathers can be collected and matched across years to identify adults that were 'recaptured'. In this way, switching behaviour and dispersal within the study site can also be defined by calculating the distance between shed feathers in consecutive years (e.g. Janowski *et al.* 2018, Hervey *et al.* 2019). There is still a problem of missing birds (feathers sampled in only 1 year), similar to resighting biases. Although there are strengths and limitations to each method surveyed here, tagging with automatic, large-scale, remote download – currently the standard GPS tracking method in wildlife telemetry with either GSM or satellite communication – provides the best data to comprehensively assess nest-switching, allowing for appropriate classification of missing birds.

CONCLUSION

As with other field methodologies, nest-switching can be estimated by different methods and in the context of different research questions. This variability introduces unavoidable complexities, rendering careful reporting of methodological decisions and consideration of inherent method-specific biases necessary for proper interpretation of the results. This will provide the means to synthesize findings across studies, towards elucidating patterns of variation in nest-switching, and its drivers and consequences.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

Sondra Turjeman: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); visualization (lead); writing–original draft (lead). **Ute Eggers:** Conceptualization (supporting); data curation (equal); methodology (equal); project administration (equal); writing–review and editing (supporting). **Shay Rotics:** Data curation (supporting); methodology (equal); writing–review and editing (supporting). **Wolfgang Fiedler:** Data curation (supporting); writing–review and editing (supporting). **Alejando Centeno-Cuadros:** Supervision (supporting); writing–review and editing (supporting). **Michael Kaatz:** Data curation (supporting). **Damaris Zurell:** Investigation (supporting); writing–review and editing (equal). **Florian Jeltsch:** Funding acquisition (equal); writing–review and editing (supporting). **Martin Wikelski:** Funding acquisition (equal); writing–review and editing (supporting). **Ran Nathan:** Conceptualization (equal); funding acquisition (equal); supervision (lead); writing–original draft (supporting).

ETHICS STATEMENT

All applicable institutional and/or national guidelines for the care and use of animals were followed: permits were acquired for all sampling areas and sampling was performed by local experts in accordance with the ethical

guidelines as approved by the Federal State of Brandenburg, Landesamt für Arbeitsschutz, Umwelt, Gesundheit und Verbraucherschutz (Brandenburg, Germany; reference numbers V3-2347-8-2012 and 2347-16-2016) and the Federal State of Sachsen-Anhalt: Landesverwaltungsamt Referat Naturschutz, Landschaftspflege (Sachsen-Anhalt, Germany; reference numbers 407.3.3/255.13-2248/2 and 407.3.3/759.12-22482/2).

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Data Availability Statement

The datasets generated and/or analysed during the current study can be found in Datasets S1–S3.

REFERENCES

Acker, P., Besnard, A., Monnat, J.Y. & Cam, E. 2017. Breeding habitat selection across spatial scales: is grass always greener on the other side? *Ecology* **98**: 2684–2697.

Ayers, C.R., Hanson-Dorr, K.C., Stromborg, K., Arnold, T.W., Ivan, J.S. & Dorr, B.S. 2019. Survival, fidelity, and dispersal of Double-crested Cormorants on two Lake Michigan islands. *Auk* **136**: 1–10.

Badyaev, A.V. & Faust, J.D. 1996. Nest site fidelity in female wild turkey: potential causes and reproductive consequences. *Condor* **98**: 589–594.

Baker, M., Nur, N. & Geupel, G.R. 2017. Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using Wrentits. *Condor* **97**: 663–674.

Barbraud, C., Barbraud, J.-C. & Barbraud, M. 1999. Population dynamics of the White Stork *Ciconia ciconia* in western France. *Ibis* **141**: 469–479.

Becker, A.J., Roeder, D.V., Husak, M.S. & Murphy, M.T. 2018. Annual survival and breeding dispersal of a migratory passerine, the Scissor-tailed Flycatcher. *J. Field Ornithol.* **89**: 22–36.

Blackmer, A.L., Ackerman, J.T. & Nevitt, G.A. 2004. Effects of investigator disturbance on hatching success and nest-site fidelity in a long-lived seabird, Leach's Storm-petrel. *Biol. Conserv.* **116**: 141–148.

Blouin, M.S. 2003. DNA-based methods for pedigree reconstruction and kinship analysis in natural populations. *Trends Ecol. Evol.* **18**: 503–511.

Blums, P., Nichols, J.D., Hines, J.E. & Mednis, A. 2002. Sources of variation in survival and breeding site fidelity in three species of European ducks. *J. Anim. Ecol.* **71**: 438–450.

Botero-Delgadillo, E., Quirici, V., Poblete, Y., Cuevas, É., Kuhn, S., Girg, A., Teltscher, K., Poulin, E., Kempenaers, B. & Vásquez, R.A. 2017. Variation in fine-scale genetic structure and local dispersal patterns between peripheral populations of a South American passerine bird. *Ecol. Evol.* **7**: 8363–8378.

Bourgeois, K., Dromzée, S. & Vidal, E. 2014. Relationships between nest-cavity and mate selection, reproductive performance and fidelity in the Mediterranean endemic Yelkouan Shearwater *Puffinus yelkouan*. *Acta Ornithol.* **49**: 9–22.

Bulut, Z., Bragin, E.A., DeWoody, J.A., Braham, M.A., Katzner, T.E. & Doyle, J.M. 2016. Use of noninvasive genetics to assess nest and space use by White-tailed Eagles. *J. Raptor Res.* **50**: 351–362.

Caballero, I.C., Bates, J.M., Hennen, M. & Ashley, M.V. 2016. Sex in the city: breeding behavior of urban Peregrine Falcons in the Midwestern US. *PLoS One* **11**: 1–16.

Carey, A.B., Horton, S.P. & Biswell, B.L. 1992. Northern spotted owls: Influence of prey base and landscape character. *Ecol. Monogr.* **62**: 223–250.

Cilimburg, A.B., Lindberg, M.S., Tewksburry, J.J. & Hejl, S.J. 2002. Effects of dispersal on survival probability of adult Yellow Warblers (*Dendroica petechia*). *Auk* **119**: 778–789.

Collias, N.E. & Collias, E.C. 2016. *Nest Building and Bird Behavior*. 2nd edn. Princeton: Princeton University Press.

Cramp, S. 1978. *Handbook of the Birds of Europe, the Middle East, and North Africa. The Birds of the Western Palearctic*. Oxford: Oxford University Press.

Culina, A., Radersma, R. & Sheldon, B.C. 2015. Trading up: the fitness consequences of divorce in monogamous birds. *Biol. Rev.* **90**: 1015–1034.

Dale, S., Steifetten, Ø., Osiejuk, T.S., Ratynska, K. & Cygan, J.P. 2006. How do birds search for breeding areas at landscape level? Interpatch movements of Ortolan Buntings. *J. Ornithol.* **147**: 153–154.

Danchin, E., Boulinier, T. & Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* **79**: 2415–2428.

Flack, A., Fiedler, W., Blas, J., Pokrovsky, I., Kaatz, M., Mitropolsky, M., Aghababyan, K., Fakriadis, I., Makrigianni, E., Jerzak, L., Azafzaf, H., Feltrup-Azafzaf, C., Rotics, S., Mokotjomela, T.M., Nathan, R. & Wikelski, M. 2016. Costs of migratory decisions: a comparison across eight White Stork populations. *Sci. Adv.* **2**: e1500931.

Forero, M.G., Donázar, J.A., Blas, J. & Hiraldo, F. 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* **80**: 1298–1310.

Fowler, A.C. 2005. Fine-scale spatial structuring in cackling Canada Geese related to reproductive performance and breeding philopatry. *Anim. Behav.* **69**: 973–981.

Garcia-Heras, M.S., Arroyo, B., Mougeot, F., Bildstein, K.L., Therrien, J.F. & Simmons, R.E. 2019. Migratory patterns and settlement areas revealed by remote sensing in an endangered intra-African migrant, the Black Harrier (*Circus maurus*). *PLoS One* **14**: 1–19.

Gauthier, G. 1990. Philopatry, nest-site fidelity, and reproductive performance in Buffleheads. *Auk* **107**: 126–132.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**: 1140–1162.

Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* **13**: 1–21.

Hansson, B., Bensch, S., Hasselquist, D. & Nielsen, B. 2002. Restricted dispersal in a long-distance migrant bird with patchy distribution, the Great Reed Warbler. *Oecologia* **130**: 536–542.

Hedlund, J.S.U., Sjösten, F., Sokolovskis, K. & Jakobsson, S. 2017. Point of no return – absence of returning birds in the otherwise philopatric Willow Warbler *Phylloscopus trochilus*. *J. Avian Biol.* **48**: 399–406.

Hervey, S.D., Barnas, A.F., Stechmann, T.J., Rockwell, R.F., Ellis-Felege, S.N. & Darby, B.J. 2019. Kin grouping is insufficient to explain the inclusive fitness gains of conspecific brood parasitism in the Common Eider. *Mol. Ecol.* **28**: 4825–4838.

Hoffman, J.I., Trathan, P.N. & Amos, W. 2006. Genetic tagging reveals extreme site fidelity in territorial male Antarctic fur seals *Arctocephalus gazella*. *Mol. Ecol.* **15**: 3841–3847.

Hoover, J.P. 2003. Decision rules for site fidelity in a migratory bird, the Prothonotary Warbler. *Ecology* **84**: 416–430.

Ilan, E.K., Bobek, O., Gal, A., Saltz, D. & Motro, U. 2019. Nest-site fidelity in Lesser Kestrels: a case of win-stay/lose-shift? *Isr. J. Ecol. Evol.* **65**: 106–110.

Itonaga, N., Köppen, U., Plath, M. & Wallschläger, D. 2011. Declines in breeding site fidelity in an increasing population of White Storks *Ciconia ciconia*. *Ibis* **153**: 636–639.

Jablonszky, M., Krenhardt, K., Markó, G., Szász, E., Hegyi, G., Herényi, M., Kötél, D., Laczi, M., Nagy, G., Rosivall, B., Török, J. & Garamszegi, L.Z. 2020. A behavioural trait displayed in an artificial novel environment correlates with dispersal in a wild bird. *Ethology* **126**: 540–552.

Janowski, S., Pürckhauer, C., Krüger, R., Tietze, D.T. & Wink, M. 2018. Recruitment rates, natal and breeding dispersal of Montagu's Harriers (*Circus pygargus*) by means of microsatellite analysis. *Open Ornithol. J.* **11**: 39–55.

Jenkins, J.M. & Jackman, R.E. 1993. Mate and nest site fidelity in a resident population of Bald Eagles. *Condor* **95**: 1053–1056.

Jenkins, J.M.A., Lesmeister, D.B., Forsman, E.D., Dugger, K.M., Ackers, S.H., Andrews, L.S., McCafferty, C.E., Pruett, M.S., Reid, J.A., Sovern, S.G., Horn, R.B., Gremel, S.A., Wiens, J.D. & Yang, Z. 2019. Social status, forest disturbance, and Barred Owls shape long-term trends in breeding dispersal distance of Northern Spotted Owls. *Condor* **121**: 1–17.

Lameris, T.K. & Kleyheeg, E. 2017. Reduction in adverse effects of tracking devices on waterfowl requires better measuring and reporting. *Anim. Biotelemetry* **5**: 1–14.

Li, J., Lv, L., Wang, P., Wang, Y., Hatchwell, B.J. & Zhang, Z. 2019. Sex-biased dispersal patterns of a social passerine: Complementary approaches and evidence for a role of spatial scale. *Biol. J. Linn. Soc.* **128**: 592–602.

McClintock, B.T. & White, G.C. 2012. From NOREMARK to MARK: software for estimating demographic parameters using mark-resight methodology. *J. Ornithol.* **152**: 641–650.

Naves, L.C., Monnat, J.Y. & Cam, E. 2006. Breeding performance, mate fidelity, and nest site fidelity in a long-lived seabird: behaving against the current? *Oikos* **115**: 263–276.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. 1998. Patterns of natal and breeding dispersal in birds. *J. Anim. Ecol.* **67**: 518–536.

Part, T. & Gustafsson, L. 1989. Breeding dispersal in the Collared Flycatcher (*Ficedula albicollis*): possible causes and reproductive consequence. *J. Anim. Ecol.* **58**: 305–320.

Payne, R.B. & Payne, L.L. 1993. Breeding dispersal in Indigo Buntings: circumstances and consequences for breeding success and population structure. *Condor* **95**: 1–24.

Ponchon, A., Choquet, R., Tornos, J., McCoy, K.D., Tveraa, T. & Boulinier, T. 2018. Survival estimates strongly depend on capture–recapture designs in a disturbed environment inducing dispersal. *Ecography* **41**: 2055–2066.

Ponnikas, S., Ollila, T. & Kvist, L. 2017. Turnover and post-bottleneck genetic structure in a recovering population of Peregrine Falcons *Falco peregrinus*. *Ibis* **159**: 311–323.

Riding, C.S. & Belthoff, J.R. 2018. Breeding dispersal by Burrowing Owls (*Athene cunicularia*) in Idaho. *J. Raptor Res.* **52**: 143–157.

Robert, A., Bolton, M., Jiguet, F. & Bried, J. 2015. The survival–reproduction association becomes stronger when conditions are good. *Proc. R. Soc. B Biol. Sci.* **282**: 20151529.

Robert, A., Paiva, V.H., Bolton, M., Jiguet, F. & Bried, J. 2014. Nest fidelity is driven by multi-scale information in a long-lived seabird. *Proc. R. Soc. B Biol. Sci.* **281**: 1–7.

Robinson, J.L. & Jones, I.L. 2014. An experimental study measuring the effects of a tarsus-mounted tracking device on the behavior of a small pursuit-diving seabird. *Behaviour* **151**: 1799–1826.

Rotics, S., Kaatz, M., Resheff, Y.S., Turjeman, S., Zurell, D., Sapir, N., Eggers, U., Flack, A., Fiedler, W., Jeltsch, F., Wikelski, M., Nathan, R. & Both, C. 2016. The challenges of the first migration: movement and behaviour of juvenile vs. adult White Storks with insights regarding juvenile mortality. *J. Anim. Ecol.* **85**: 938–947.

Rotics, S., Kaatz, M., Turjeman, S., Zurell, D., Wikelski, M., Sapir, N., Eggers, U., Fiedler, W., Jeltsch, F. & Nathan, R. 2018. Early arrival at breeding grounds: causes, costs and a trade-off with overwintering latitude. *J. Anim. Ecol.* **87**: 1627–1638.

Rotics, S., Turjeman, S., Kaatz, M., Resheff, Y.S., Zurell, D., Sapir, N., Eggers, U., Fiedler, W., Flack, A., Jeltsch, F., Wikelski, M. & Nathan, R. 2017. Wintering in Europe instead of Africa enhances juvenile survival in a long-distance migrant. *Anim. Behav.* **126**: 79–88.

Rotics, S., Turjeman, S., Kaatz, M., Zurell, D., Wikelski, M., Sapir, N., Fiedler, W., Eggers, U., Resheff, Y.S., Jeltsch, F. & Nathan, R. 2021. Early-life behavior predicts first-year survival in a long-distance avian migrant. *Proc. R. Soc. B* **288**: 1942.

Rushing, C.S., Hostetler, J.A., Sillett, T.S., Marra, P.P., Rotenberg, J.A. & Ryder, T.B. 2017. Spatial and temporal

drivers of avian population dynamics across the annual cycle. *Ecology* **98**: 2837–2850.

Sandercock, B.K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. *J. Wildl. Manage.* **70**: 1504–1520.

Sandercock, B.K., Beissinger, S.R., Stoleson, S.H., Melland, R.R. & Hughes, C.R. 2000. Survival rates of a neotropical parrot: implications for latitudinal comparisons of avian demography. *Ecology* **81**: 1351–1370.

Saunders, D.A., White, N.E., Dawson, R. & Mawson, P.R.M. 2018. Breeding site fidelity, and breeding pair infidelity in the endangered Carnaby's cockatoo *Calyptorhynchus latirostris*. *Nat. Conserv.* **27**: 59–74.

Schwarz, C.J. & Seber, G.A.F. 1999. Estimating animal abundance: review III. *Stat. Sci.* **14**: 427–456.

Sergio, F., Tanferna, A., Blas, J., Blanco, G. & Hiraldo, F. 2019. Reliable methods for identifying animal deaths in GPS- and satellite-tracking data: review, testing, and calibration. *J. Appl. Ecol.* **56**: 562–572.

Serrano, D., Tella, J.L., Forero, M.G. & Donázar, J.A. 2001. Factors affecting breeding dispersal in the facultatively colonial Lesser Kestrel: individual experience vs. conspecific cues. *J. Anim. Ecol.* **70**: 568–578.

Severson, J.P., Coates, P.S., Prochazka, B.G., Ricca, M.A., Casazza, M.L. & Delehanty, D.J. 2019. Global positioning system tracking devices can decrease Greater Sage-grouse survival. *Condor* **121**(3): duz032.

Shaw, A.K. & Levin, S.A. 2013. The evolution of intermittent breeding. *J. Math. Biol.* **66**: 685–703.

Shields, W.M. 1984. Factors affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). *Auk* **101**: 780–789.

Spendelow, J.A. & Eichenwald, A.J. 2018. Rapid departure of Roseate Terns (*Sterna dougallii*) following large-scale nest failure. *Wilson J. Ornithol.* **130**: 485–492.

Stow, A.J. & Sunnucks, P. 2004. High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Mol. Ecol.* **13**: 419–430.

Strickland, B.K., Dorr, B.S., Pogmore, F., Nohrenberg, G., Barras, S.C., McConnell, J.E. & Gobeille, J. 2011. Effects of management on Double-crested Cormorant nesting colony fidelity. *J. Wildl. Manage.* **75**: 1012–1021.

Sumasgutner, P., Terraube, J., Coulon, A., Villers, A., Chakarov, N., Kruckenhauser, L. & Korpimäki, E. 2019. Landscape homogenization due to agricultural intensification disrupts the relationship between reproductive success and main prey abundance in an avian predator. *Front. Zool.* **16**: 1–14.

Tolvanen, J., Pakanen, V.M., Valkama, J. & Tornberg, R. 2017. Apparent survival, territory turnover and site fidelity rates in Northern Goshawk *Accipiter gentilis* populations close to the northern range limit. *Bird Study* **64**: 168–177.

Turjeman, S., Centeno-Cuadros, A., Eggers, U., Rotics, S., Blas, J., Fiedler, W., Kaatz, M., Jeltsch, F., Wikelski, M. & Nathan, R. 2016. Extra-pair paternity in the socially monogamous White Stork (*Ciconia ciconia*) is fairly common and independent of local density. *Sci. Rep.* **6**: 27976.

Vergara, P., Aguirre, J.I., Fargallo, J.A. & Davila, J.A. 2006. Nest-site fidelity and breeding success in White Stork *Ciconia ciconia*. *Ibis* **148**: 672–677.

Weiser, E.L., Lanctot, R.B., Brown, S.C., Gates, H.R., Bentzen, R.L., Bêty, J., Boldenow, M.L., English, W.B., Franks, S.E., Koloski, L., Kwon, E., Lamarre, J.-F., Lank, D.B., Liebezeit, J.R., McKinnon, L., Nol, E., Rausch, J., Saalfeld, S.T., Senner, N.R., Ward, D.H., Woodard, P.F. & Sandercock, B.K. 2018. Environmental and ecological conditions at Arctic breeding sites have limited effects on true survival rates of adult shorebirds. *Auk* **135**: 29–43.

White, G.C. & Burnham, K.P. 1999. Program mark: survival estimation from populations of marked animals. *Bird Study* **46**: S120–S139.

Williams, T.D. & Rodwell, S. 1992. Annual variation in return rate, mate and nest-site fidelity in breeding Gentoo and Macaroni Penguins. *Condor* **94**: 636–645.

Zurell, D., von Wehrden, H., Rotics, S., Kaatz, M., Groß, H., Schlag, L., Schäfer, M., Sapir, N., Turjeman, S., Wikelski, M., Nathan, R. & Jeltsch, F. 2018. Home range size and resource use of breeding and non-breeding White Storks along a land use gradient. *Front. Ecol. Evol.* **6**: 79.

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SUPPORTING INFORMATION

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

Appendix S1. Literature Review.
Appendix S2. Case Study Supplement.
Data S1. Raw data - ringing datasets.
Data S2. Raw data - genotypes (genetic dataset).
Data S3. Raw data - tagging datasets.