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

SONDRA TURJEMAN,†* UTE EGGERS,‡ SHAY ROTICS,† WOLFGANG FIEDLER,§ ALEJANDRO CENTENO-CUADROS,† MICHAEL KAATZ,‖ DAMARIS ZURELL,§ DR. FLORENTIN JELTSCH‡, ALLEJANDRO CENTENO-CUADROS,† MARTIN WIKELSKI§ & RAN NATHAN†*

1Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem, 91904, Israel
2Department of Plant Ecology and Nature Conservation, Institute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, Potsdam, 14469, Germany
3Department of Migration and Immuno-Ecology, Max-Planck-Institute for Ornithology, D-78315, Radolfzell, 78315, Germany
4Department of Biology, University of Konstanz, Konstanz, D-78468, Germany
5Vogelschutzwarte Storchenhof Loburg e.V., Chausseestr. 18, Loburg, D-39279, Germany
6Dynamic Macroecology, Department of Landscape Dynamics, Swiss Federal Research Institute WSL, Birmensdorf, 8903, Switzerland
7Berlin-Brandenburg, Institute of Advanced Biodiversity Research (BBIB), Berlin, D-14195, Germany

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 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,

| Box 1: Definitions of true and confounding components of nest-switching behaviour with examples from the presented case study |
| Breed 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 km²), 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. |
Thus, some researchers estimate a
persal (LDD; Cilimburg
ignored, making samples a biased representation of the
long-distance switches. In many studies, missing birds are
switching and the latter underestimates it by ignoring
the 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
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 stud-
ies of switching, fidelity and breeding dispersal, particu-
larly 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 & Rod-
well 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 & Gustaf-
sson 1989, Forero et al. 1999, Serrano et al. 2001, Her-
vye et al. 2019, Ilan et al. 2019). Often these decisions
must be extrapolated (Danchin et al. 1998, Tolvanen

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, Cabal-
lero et al. 2016). Many nests can be sampled non-inva-
sively or with minimal trapping effort, but genetic
analyses can be expensive and, without extensive sam-
ping, 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-pro-
hibitive, and may negatively affect fitness and beha-
viour (Lameris & Kleyheeg 2017, Severson et al.
2019). Finally, it can be difficult to reliably differenti-
ate 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 esti-
mates, 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 & Jack-
man 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 dis-
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
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 stud-
ies of switching, fidelity and breeding dispersal, particu-
larly 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 & Rod-
well 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 & Gustaf-
sson 1989, Forero et al. 1999, Serrano et al. 2001, Her-
vye et al. 2019, Ilan et al. 2019). Often these decisions
must be extrapolated (Danchin et al. 1998, Tolvanen

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 crite-
rion.

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 over-
lap across methods (Fig. 1). An umbrella project encom-
passed studies of migration (GPS; Flack et al. 2016, Rotics
(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.
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 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’, ‘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 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

---

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

<table>
<thead>
<tr>
<th>Comparison</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>Switch rate</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ring1</td>
<td>743</td>
<td>369</td>
<td>–</td>
<td>0.3318</td>
<td>1112 (408)</td>
</tr>
<tr>
<td>Ring2</td>
<td>743</td>
<td>96</td>
<td>–</td>
<td>0.1144</td>
<td>839 (408)</td>
</tr>
<tr>
<td>Genetics</td>
<td>55</td>
<td>30</td>
<td>11</td>
<td>0.2708</td>
<td>96</td>
</tr>
<tr>
<td>Tag1</td>
<td>67</td>
<td>40</td>
<td>–</td>
<td>0.3738</td>
<td>107 (51)</td>
</tr>
<tr>
<td>Tag2</td>
<td>67</td>
<td>20</td>
<td>–</td>
<td>0.2299</td>
<td>87 (39)</td>
</tr>
</tbody>
</table>

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).
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.

We would like to acknowledge the contribution of all volunteers and ringers who assisting in sample collection, including Michael Arens, Joerg Dummer, Mario Firla, Thomas König, Thoralf Schaffer, Falk Schulz, Bernd Weisbach, Alexandra Hinz, Roxana Grohnert, Jan Philipp Wevers, Simon, Jens Lehmann, Karin Spaeth, Anne Schindelm, Merlin Schaefer, Robert Sieg, Dete Krüger and Esther Bazant. We would also like to express our gratitude to Meira Shlepakov of the Hebrew University Center for Genomic Technologies for her genotyping work, Ron Efrat for help with data processing, and Nadav Ganot with Sasha Pekarsky for help with map-generation and QGIS.

**CONFLICT OF INTEREST**

The authors declare that they have no competing interests.

**Table 2.** Methods employed to assess nest-switching.

<table>
<thead>
<tr>
<th>Method</th>
<th>Filtration options</th>
<th>Strengths</th>
<th>Limitations</th>
<th>Improvements</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ringing</td>
<td>Found in at least one of two consecutive years</td>
<td>Inexpensive, large proportion of population easily tracked, long-term data can be obtained retroactively.</td>
<td>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.</td>
<td>Study specific data collection rather than retroactive collation, inclusion of a search buffer beyond the focal population’s breeding range.</td>
</tr>
<tr>
<td>GPS tagging</td>
<td>Data in at least one of two consecutive years</td>
<td>High-resolution movement data without observation effort, track multiple years, remote data download can help differentiate dispersal from death.</td>
<td>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.</td>
<td>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.</td>
</tr>
<tr>
<td>Genetic testing</td>
<td>Adult feathers retrieved in at least one of two consecutive years</td>
<td>Sample non-invasively/only offspring, uncover EPP, breeding output data for many mating pairs.</td>
<td>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.</td>
<td>Costs of whole genome sequencing and genotyping by sequencing are decreasing, improved kinship assignment allows application in non-model species.</td>
</tr>
</tbody>
</table>

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

**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). Alejandro 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 407.3.3/759.12-2248/2).

FUNDING

This research was funded by DIP grants (DFG) NA 846/1-1 and WI3576/1-1 to R.N., F.J. and M.W. S.T. was supported by a doctoral scholarship from the Clore Foundation. We also acknowledge financial support from the Adelina and Massimo Della Pergola Chair in the framework of the BioMove Research Training Group to F.J.

Data Availability Statement

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

REFERENCES


Received 25 October 2020; Revision 14 January 2021; revision accepted 21 January 2021. Associate Editor: Dominic McCafferty.

**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 - tagging datasets.

Data S2. Raw data - genotypes (genetic dataset).

Data S3. Raw data - tagging datasets.