Nest-site detection and estimation of avian reproductive outcome from GPS-tracking data

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Running headline: Estimating avian reproductive outcome from GPS-tracking data

Abstract

Movement ecology is flourishing thanks to advancements of tracking technology and, in parallel, a proliferation of methods to infer behavior from individual trajectories. An emerging direction is the use of telemetry data to estimate reproductive success, which connects movement to components of individual fitness. Here, we introduce a method to locate breeding attempts and estimate their outcome from avian GPS-tracking data, implemented in the R package 'nestR'. We identified nest sites based on the analysis of recursive movements of breeding individuals acting as central place foragers. Using trajectories with known breeding attempts, we estimated a set of species-specific criteria for the identification of nest sites, which we further validated using non-reproductive individuals as controls. We then estimated individual nest survival as a measure of reproductive outcome from nest-site re-visitation histories during breeding attempts, using a Bayesian hierarchical modeling approach that accounted for temporally variable re-visitation patterns, probability of visit detection, and missing data. We illustrated the application of our method and evaluated its performance using data for three species: wood storks (*Mycteria americana*), lesser kestrels (*Falco naumanni*), and Mediterranean gulls (*Ichthyaetus melanocephalus*). Across the three species, positive predictive value of the nest-site detection algorithm was between 73-100% and sensitivity was between 87-92%, and we correctly estimated the outcome of 86-100% breeding attempts. Our method can be broadly applied to estimate individual reproductive outcome in a variety of central place foragers, bridging the gap between movement behavior, environmental factors, and their fitness consequences.

Key-words

birds – fitness – GPS telemetry – movement ecology – nest survival – nestR – R package

Introduction

A major goal of movement ecology is to uncover behaviors underlying, and thus shaping, movement trajectories (Nathan et al., 2008; Schick et al., 2008; Wilmers et al., 2015). Knowing what animals are doing when moving a certain way can improve our understanding of the links between movement and resource dynamics, species interactions, distribution, and individual fitness (Mueller & Fagan, 2008; Schick et al., 2008; Morales et al., 2010). Given the central role of fitness in ecological and evolutionary processes, estimating it from movement patterns is a long-sought goal (Morales et al., 2010; Singh & Ericsson, 2014). Specifically, connecting movement to reproduction, an important component of fitness, is a promising emerging application. For example, recent studies used changes in movement patterns to detect parturition events along ungulate GPS tracks, particularly moose (*Alces alces*; Severud et al., 2015; Nicholson et al., 2019) and caribou (*Rangifer tarandus*; DeMars, Auger Méthé, Schlägel, & Boutin, 2013; Bonar, Ellington, Lewis, & Vander Wal, 2018). However, to our knowledge, no study has attempted to infer avian reproductive fitness from movement data.

Recursive movement patterns can reveal when and where birds are breeding, and whether they are successful. Recursive movements are repeated returns to a same location, and they are indicative of places of ecological relevance for many taxa, such as dens, nests, and foraging patches (Berger-Tal & Bar-David, 2015; Bracis, Bildstein, & Mueller, 2018). Recursive movement patterns can also provide insight into life-history: some animals are tied to specific locations in specific phases of their life cycle and exhibit recursive movements to and from those locations (Bracis et al., 2018). These include altricial birds. While breeding, altricial bird species act as central place foragers (*sensu* Orians & Pearson, 1979), recursively departing from their nest site to embark on foraging trips and returning to incubate eggs or provide food for nestlings (Andersson, 1981; Alonso, Carrascal, Muñoz-Pulido, & Alonso, 1994; Burke & Montevecchi, 2009). Back-and-forth trips can therefore be observed in movement data and potentially used to identify when and where a bird is nesting. Once the location of

a nest has been identified, patterns of nest-site re-visitation may reveal information about the fate of a breeding attempt and may be used to infer reproductive outcome.

Estimating avian reproductive outcome from tracking data can have advantages over conventional field methods. For example, it could be valuable whenever gathering data on reproductive outcome through direct observation is logistically difficult or causes excessive disturbance (Etterson et al., 2011; Wilmers et al., 2015; Nicholson et al., 2019). Moreover, linking reproductive outcome to foraging conditions can be challenging when nests are monitored in the field and researchers do not have information on locations visited by birds away from the nest. Inferring reproductive outcome from movement would allow researchers to directly relate components of individual fitness to environmental conditions experienced by birds not only at the nest but also at other locations used during breeding, by coupling tracking data with remote sensing (Cagnacci, Boitani, Powell, & Boyce, 2010; Pettorelli et al., 2014).

Here, we introduce a data-driven method to locate breeding attempts along movement trajectories of altricial bird species and estimate their outcome based on patterns of nest re-visitation. We demonstrate the broad applicability of our approach by illustrating its use on GPS-tracking data for three species differing in their breeding habitat and ecology: wood storks (*Mycteria americana*), lesser kestrels (*Falco naumanni*), and Mediterranean gulls (*Ichthyaetus melanocephalus*).

Materials and Methods

Method description

Nest-site detection – Our workflow is composed of two parts: first, the detection of nest sites, and second, the estimation of reproductive outcome (Figure 1). Nest sites are identified as repeatedly visited locations along individual trajectories (Figure 1). Returns to a location are defined as returns to a circular area of a user-defined radius buffering each point of the trajectory. Using buffers accounts for

the spatial scattering of GPS points around a location due to both behavior and GPS error (Frair et al., 2010). The buffer size sets the spatial scale at which re-visitation patterns are calculated and is chosen according to the expected scale of movements, which should be small in the case of a nest (compared, for example, to returns to a same foraging area but not exact location). Re-visitation patterns are described by the following set of parameters: the maximum number of consecutive days a location is visited; the percentage of days it is visited between the first and last visit; and the percent fixes at a location on the day with maximum attendance. Each re-visited location is a potential nest site. Parameter values are then used as diagnostic features to filter actual nest sites among re-visited locations, based on the rationale that re-visitation patterns differ between nest and non-nest sites. Nest sites are often visited for longer stretches of consecutive days, on more days, and more frequently or for longer within a day than other types of re-visited locations. The parameters we use to describe re-visitation patterns are meant to capture these diagnostic behaviors and identify nest sites among re-visited locations. Combined, an appropriate buffer size and the thresholds imposed for re-visitation parameters should isolate breeding behavior from other types of repetitive movements such as foray search (Conradt, Zollner, Roper, Frank, & Thomas, 2003) and territoriality (Brown, Stouffer, & Strong, 2000). The method can be tailored to different case studies by restricting the analysis within the breeding season for a given species and accounting for data sampling rate and fix failure rate.

Unless prior knowledge is available about re-visitation patterns to nest sites, researchers will need ways to inform their choice of parameter values used for identifying nest sites among re-visited locations (Figure 1). If the true location of nests is known for a subset of the data, researchers can compare re-visitation patterns at known nest sites to those of non-nest sites and find one or more sets of parameter values to discriminate between them. If on-ground data are not directly available, an alternative is to visually explore the data and identify trusted nest sites, where possible. For example, likely nest sites may be recognized in some species based on habitat features or proximity to known

breeding colonies. Once known or trusted nest sites are identified, non-nest sites can be selected based on a criterion of temporal overlap; locations re-visited simultaneously with a breeding attempt can be considered non-nest sites, assuming birds cannot breed in two places at the same time (which may not be true in all study systems).

Several approaches are possible to identify sets of parameter values to distinguish nest from non-nest sites. We propose one based on classification and regression trees (CART; De'ath & Fabricius, 2000). We apply CART to a dataset of known nest and non-nest sites, and prune the tree to the optimal number of nodes based on a minimum relative error criterion (De'ath & Fabricius, 2000). More sophisticated classification tools, such as random forests (Breiman, 2001), may also be appropriate for this task, but CART has the advantage of providing outputs that are easy to interpret biologically. CART identifies one or more sets of parameter values that best discriminate between nest and non-nest sites, which is then applied to the complete set of re-visited locations to identify nest sites among them (Figure 1). In case of temporal overlap between breeding attempts that satisfy the criteria, and again assuming birds cannot breed in two places at the same time, the recommended option is to pick the most visited candidate and discard the rest. For each nest site, we compile a history of nest re-visitation, in the form of a presence/absence time series (0/1 for each GPS point), which is then used to estimate the outcome of each breeding attempt.

Reproductive outcome estimation – The outcome of each identified breeding attempt is estimated using a Bayesian hierarchical modeling approach (Figure 1). We define success as survival of at least one nestling until fledging and failure to none. A breeding attempt is considered successful if the nest site was visited until the end of a complete breeding cycle for the focal species, which includes nest-building, egg-laying, incubation, and chick-rearing until the nestlings reach autonomy and no longer receive parental care. Nest survival is estimated based on patterns of nest-site re-visitation,

taking into account imperfect detection of nest visits and missing fixes. The MCMC algorithm is implemented in JAGS (Plummer, 2003) via the R package 'rjags' (Plummer, 2018).

The model specification includes two processes: the survival process, which is not directly observable, and the observation process, which is the re-visitation history. Much like a Bayesian implementation of a Cormack-Jolly-Seber capture-mark-recapture model (Lebreton, Burnham, Clobert, & Anderson, 1992; Schaub & Royle, 2014), the latent nest survival variable, *z*, is modeled as a Bernoulli variable at the daily scale as a function of survival status and daily survival probability, *φ*, at the previous time-step:

$$z_t \sim Bern(z_{t-1} \times \phi_{t-1})$$

Observed visits on a given day are modeled as a binomial variable as a function of current nest survival status, probability of visit detection, *p*, and number of GPS fixes available, *N*, on day *t*:

$$Y_t \sim Bin(N_t, z_t \times p_t)$$

Where the probability of detection is a function of N and conditional to the nest being alive on that day:

$$p_t = Pr(visit\ detected | z_t = 1, N_t)$$

Reproductive outcome is defined as the probability *P* that the nest was still surviving on the last day of the theoretical duration of a complete breeding attempt, *T*:

$$P = Pr(z_T = 1)$$

Both survival and detection probability are modeled using a binomial Generalized Linear Model as a function of the day of the attempt:

$$logit(\phi_t) = \beta_{\phi_0} + \beta_{\phi_1} \times t$$

$$logit(p_t) = \beta_{p_0} + \beta_{p_1} \times t$$

The model is fully specified by using uninformative priors on the β parameters, in this case a normal distribution with a mean of 0 and precision of 1e-5. In the current implementation, daily survival and detection are assumed to be the same for all nests in the population. The model outputs daily estimates of survival and detection probability at the population level, as well as daily survival estimates for each breeding attempt along with credible intervals.

Assumptions underlying this model include: birds are tracked for the entire duration T of a complete nesting attempt (if birds were tagged part-way through an attempt, T needs to be adjusted by subtracting the age of the nest (in days) at tagging); the GPS tag does not permanently fail before the end of the attempt; parents visit the nest until fledging, or nestling mortality is negligible between the time when parental care is interrupted and fledging; parents stop visiting a nest after failing.

Software description

Our method is implemented in the R package 'nestR' (https://github.com/picardis/nestR; Picardi, Smith, Boone, & Basille, 2019). The package includes functions to implement each step of the described workflow (Figure 1). The function ‘find_nests()’ is used to identify re-visited locations and nest sites among them. An interactive visualization tool for dynamic exploration of re-visited locations is available in the form of a Shiny application launched by the function ‘explore_nests()’. Exploratory data on nest and non-nest sites is compiled using the function ‘get_explodata()’ and used to identify parameter values for the detection of nests using the function ‘discriminate_nests()’. Once nests are identified, re-visitation histories are formatted using the function ‘format_attempts()’ for input in ‘estimate_outcomes()’, the function for estimating the outcome of breeding attempts. The package also includes several functions for plotting and summarizing results (‘summarize_outcomes()’, ‘plot_nest_surv()’, ‘plot_survival()’, ‘plot_detection()’; Figure 1). For a thorough description of package structure and features, we direct the reader to the 'nestR' package vignette.

Study cases

We applied our method to GPS-tracking data for 148 individual-years for wood storks (henceforth storks), 56 for lesser kestrels (henceforth kestrels) and 29 for Mediterranean gulls (henceforth gulls; Table 1). All tags were solar-powered and recorded fixes primarily during daytime. Details about devices, settings, harnesses, and study areas regarding storks and kestrels can be found in Borkhataria, Frederick, Hylton, Bryan, & Rodgers (2008) and Cecere et al. (2018), respectively. To find nest sites, we restricted the analysis to the breeding season only for each species (Table 1). While both kestrels and gulls have a well-defined breeding season between April and August in our study areas (Snow, Perrins, Hillcoat, Gillmor, & Roselaar, 1997), storks in the southeastern U.S. can breed at slightly different times of the year depending on latitude (Coulter, Rodgers, Ogden, & Depkin, 1999); Table 1). In this case, we used a conservative approach and only excluded the period where no breeding activities were expected to occur anywhere in the range.

Given the spatial resolution of the GPS data (Table 1) and the expected scale of movements around the nest site for all three species, we used a buffer of 40 m around each GPS position. We initially screened trajectories for any re-visited locations using non-constraining values for parameters describing re-visitation patterns (thus not applying any filtering). We then used on-ground data on known nest locations to select true nests and non-nest sites from the re-visited locations. Kestrels and gulls were captured at the nest site (Table 1), so the location of the nest was known. For storks, on-ground data on nest locations was available for 10 individual-years (Bear D., unpublished data). We explored the remaining stork trajectories and identified those for which the top visited location was at a known breeding colony (data from U.S. Fish and Wildlife Service 2018). We marked these as trusted and treated them as known nest sites for the rest of the analysis.

We used CART to compare re-visitation patterns between nest and non-nest sites, and used the resulting sets of parameter values to filter nest sites among re-visited locations in the trajectories of breeding individuals. We only retained individual-years where data exceeded the minimum number of

consecutive days visited indicated by CART (Table 1). Even when CART did not suggest that the number of consecutive days visited was an important predictor of true nest sites, we chose a reasonable value to use as a threshold for this parameter, as we did not expect to have enough power to discern nest from non-nest sites for attempts that failed in the first handful of days. We only retained the candidate with the most visits among any sets of breeding attempts that were temporally overlapping. We used non-breeder trajectories (sub-adults in the case of storks, non-breeding season data in the case of kestrels and gulls) to validate our results against false positives. We calculated positive predictive value of our algorithm as the percentage of nest sites that were known among those we found for each species; sensitivity as the percentage of known nest sites that were identified; false negative rate as the percentage of known nest sites that we failed to identify; and false positive rate as the percentage of non-breeding individual-years for which we erroneously identified a nest site.

We fit the nest survival model described above to estimate the outcome of identified breeding attempts, using only individual-years for which the tag was active throughout the attempt to meet model assumptions (Table 1). Since kestrels and gulls were captured after they had already started breeding (immediately after hatching and in late incubation, respectively, although the exact age of the nest at tagging was unknown), the initial part of every breeding attempt was missing from the data. To account for this, we subtracted the theoretical number of days until hatching (for kestrels, 25 days) and late incubation (for gulls, 20 days) from the value of T (Table 1). We evaluated performance of the method by comparing survival estimates to known outcomes.

Results

The initial screening with no filtering identified 9871 re-visited locations (i.e., potential nest sites) for storks, 511 for kestrels, and 1379 for gulls. Results from CART showed that the optimal set of parameter values to discriminate nest from non-nest sites was 14 minimum consecutive days visited

and 79% minimum nest attendance on the top day for storks, 7 minimum consecutive days visited for kestrels, and 26% minimum attendance on the top day for gulls (Figure 2). Because CART did not indicate a minimum number of consecutive days visited for gulls, we added a reasonable constraint for this value by exploring the data and determining which value would allow us to rule out most non-nest sites while retaining most nest sites (8 days; Table 2). By filtering re-visited locations using these parameter values, we identified 109 nest sites for storks, 45 for kestrels, and 30 for gulls, which closely matched the number of nest sites we were expecting to find (Table 1). As a consequence, the positive predictive value of the algorithm ranged between 73-100%, the sensitivity between 87-92%, and the false negative rate between 8-12% for the three species (Table 3). The false positive rate was 7% for storks and 0% for gulls but reached 44% for kestrels (Table 3). The probability of detecting nest visits decreased throughout the breeding attempt for all three species, while survival remained constant (Figure 3). We correctly estimated the outcome of 100% of breeding attempts for gulls and 86% for kestrels (1 failure and 2 successes incorrectly estimated; Figure 4). No data on true outcomes were available for storks, therefore we were unable to verify survival estimates for this species.

Discussion

We presented a data-driven method to identify nest-site locations of altricial avian species and estimate the outcome of breeding attempts based on GPS-tracking data. This is among the first attempts to infer the reproductive component of fitness from telemetry data (DeMars et al., 2013), and to our knowledge, the first applied to birds. We demonstrated the broad applicability of our method by illustrating its use on GPS-tracking data from three species which differ in their breeding behavior and ecology, including a subtropical wading bird, a small steppe raptor, and a seabird.

Nest-site detection – Our nest-site detection method performed well for all three species, allowing us to correctly identify most or all known nest sites from movement trajectories of breeding

individuals. As a cautionary note for interpreting nest detection results, we reiterate that most nest locations we treated as known for storks were trusted nest sites for which we did not have on-ground confirmation but that were located in known colonies (97 out of 107). We achieved high positive predictive value (73-100%) and sensitivity (87-92%) for all species. Importantly, the positive predictive value quantifies how many of the nest sites we found were known, which does not necessarily imply that the remaining were non-nest sites: it is possible that those we were unable to confirm for storks and gulls included second attempts (true but unknown nest sites) in addition to non-nest sites, as both species may attempt to breed again at a different location if their first clutch fails early in the season. In support of this possibility, all unknown nest sites we found for gulls were from birds whose known attempt failed early on, and they were thus plausible second attempts. The same might be true for storks, although we did not have on-ground data to confirm it. False negative rates were low for all species (8-12%) and mostly associated with early failures: 2 out of 2 nest sites that we failed to identify for gulls and 2 out of 5 for kestrels corresponded to attempts that failed before the enforced limit of consecutive days visited (as early as the day after tagging in the case of gulls). This may be true for storks as well, where the breeding attempts we were unable to identify might have failed before the 14-day mark. Not identifying breeding attempts whose duration does not exceed the minimum constraint applied is a logical implication of the approach rather than a failure of the algorithm. The remaining 3 nest sites that we were unable to identify for kestrels did not fail within the first week, but were never visited for 7 consecutive days. False positives were none or negligible for gulls and storks (0% and 7% respectively), but reached 44% for kestrels. This is likely explained by species-specific behavior: non-breeding kestrels spend long stretches of time and consecutive days on a perch while scanning for prey or resting. Distinguishing these patterns of attendance and re-visitation from those of a nest might be challenging without applying restrictions based on seasonality and geographical area (e.g., breeding versus wintering range).

Error rates for nest-site identification vary in importance depending on the study objectives. If the objective is to estimate reproductive outcome, ensuring that attempts are not missed should receive priority over avoiding the selection of non-nest sites. Any re-visited location that gets erroneously identified as a nest site would likely be classified as a failed attempt eventually anyway. In this case, we suggest that researchers may want to focus on minimizing false negatives. Conversely, if the objective of a study is, for instance, to analyze factors associated with nest-site selection, minimizing false positives should be the priority.

Once on-ground data on nest locations are used to identify parameter values to distinguish nests among re-visited locations, these parameter values can then be applied to new individuals of the same species for which on-ground information is not available, assuming other data characteristics are the same. If CART is the tool of choice to inform the choice of parameter values, we recommend that classification thresholds in output should be used with caution, and considered more as range indications than as clear-cut rules. We also recommend that parameter values suggested by CART should be critically evaluated for their biological significance before use, and that adjustments should be made as needed based on knowledge of the species biology. Future efforts to improve our method for the identification of nest locations will include incorporating uncertainty in our estimates of nest sites, allowing us to interpret classification results in a probabilistic framework.

Reproductive outcome estimation – We correctly estimated reproductive outcome of 100% of breeding attempts for gulls and 86% for kestrels, with probability of success estimated as $P > 0.97$ for true successes and as $P = 0$ for true failures. The remaining attempts were two successes that we estimated as failures ($P <= 0.3$) and one failure that we estimated as a success ($P = 0.98$). The two attempts that we erroneously estimated as failures corresponded to one male and one female kestrel whose original clutch included four eggs and was partially lost, leading to two and one fledglings, respectively. When the brood is reduced, remaining nestlings may grow more rapidly and lead to a

faster completion of the breeding cycle, which may have compromised our ability to detect these attempts as successful as they did not reach the benchmark $T = 60$. Specifically, one of the two attempts was completed within 27 days of tagging, which corresponds to $T = 52$. However, the other attempt was completed within 33 days of tagging, corresponding to $T = 58$, which is a similar duration to other successful attempts that we estimated correctly. In this case, our inability to recognize the attempt as successful might have depended on behavioral differences between parents, whereby the male we were tracking might have interrupted parental care before the female did. This result highlights the importance of taking into account sex differences in breeding behavior, where that applies. For example, in species exhibiting uniparental care, inference should only be based on the sex that carries out parental care. The failed attempt that we erroneously estimated as successful corresponded to a male that occasionally visited the nest site after failing, thus violating one of the assumptions of our model. Unfortunately, this was the only failed attempt for kestrels in our dataset, which makes it difficult to generalize our ability to estimate nest failures for this species. Overall, the three instances of incorrect estimation might suggest that model assumptions, such as interruption of nest visits after failure, might not always hold across species; or that the duration of a complete breeding cycle may be too variable to lend itself to generalizations in some species; or that not knowing the exact age of the nest at tagging might have reduced our power to distinguish late failures from successful attempts that were completed in less-than-average time.

We did not have on-ground data to validate our estimation of reproductive outcome for storks; however, most attempts were estimated as either $P = 1$ or $P = 0$, while intermediate values (between 0.25 and 0.75) were relatively rare (14 out of 109). This is an important result given that data for storks were at lower temporal resolution compared to kestrels and gulls (Table 1). Low temporal resolution of data in combination with decreasing frequency of nest visits can, in principle, increase the uncertainty of outcome estimation by reducing probability of visit detection especially towards the end of a

breeding attempt (Figure 3). Thus, the higher proportion of intermediate values for estimates of breeding success probabilities we observed in storks compared to kestrels and gulls was to be expected, but results were still rather polarized, suggesting that the method is largely able to distinguish between successes and failures at this temporal resolution, given the frequency of nest visits in storks.

Synthesis and significance – The most important implication of our work is the ability to use telemetry data to obtain estimates of bird reproductive outcome. Reproductive outcome is an important component of fitness, and estimating it from tracking data will help establish the long-sought bridge between movement and fitness at the individual level (Nathan et al., 2008; Morales et al., 2010). Our method allows researchers to obtain critical information on reproductive outcome for birds that nest in remote or inaccessible locations where it is difficult or risky to collect on-ground data (Götmark, 1992; Mayer-Gross, Crick, & Greenwood, 1997; Etterson et al., 2011; Wilmers et al., 2015). Information on reproductive outcome obtained from tracking data can also be combined with environmental conditions experienced by individual birds, not only at the nest but in other important locations visited during breeding attempts, such as foraging grounds (Cagnacci et al., 2010; Pettorelli et al., 2014). This opens new research avenues regarding links between components of individual fitness, movement strategies, and habitat. Important exceptions to the applicability of our method are precocial species and nest parasites, where parental care is limited or absent. Another limitation of our approach is that it does not provide estimation of reproductive success in terms of number of offspring, but only in terms of overall success or failure. Under this aspect, our method does not compare to the level of detail obtainable with conventional field methods.

Besides estimating reproductive outcome, our method is useful as a tool to identify nest-site locations. Identifying nest sites is valuable in and of itself: for example, it may allow researchers to find previously unknown nesting sites in species for which breeding locations are partly or entirely unknown.

Overall, our method can appeal to researchers with different objectives. First, it may be useful to researchers that want to investigate reproductive outcome in relation to movement and environmental factors away from the nest. Second, it may serve researchers that want to obtain data on reproductive outcome for species that are not easy to monitor on the ground. Third, it may be of use to researchers that want to identify the location of nest sites for analyses of breeding site fidelity, nest-site selection, or discovery of new breeding sites. Our method can be applied both in situations of opportunistic use of historical tracking data or in cases where the study is explicitly designed with these objectives in mind. Conservation and management applications may both benefit from the availability of our method and its implementation in an open-access, user-friendly R package, 'nestR'. Knowledge of the biology and ecology of the target species and careful consideration of data characteristics and limitations are critical for successful use of the tools we presented. As technology improves and tracking devices are miniaturized, our method will allow researchers to identify nest sites and estimate reproductive outcome of an increasingly broad variety of avian species.

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Authors’ Contributions

S. Picardi conceived the idea. S. Picardi., B. J. S., and M. E. B. implemented the analyses. S. Picardi wrote the paper. M. B. and P. C. F. supervised research. J. G. C., D. R., L. S., S. Pirrello, and R. R. B. collected the data. All authors contributed to revisions.

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Figures and Tables

Table 1 – Differences among GPS-tracking datasets for wood storks, lesser kestrels, and Mediterranean gulls in terms of sample sizes, data characteristics, and species seasonality and ecology.

		Wood stork	Lesser kestrel	Mediterranean gull
Spatial resolution (m)		18	<10	<10
Temporal resolution (min)		60	15 (summer)/30 (winter)	15
Fix failure rate		High	Low	Low
Tagged at		Fledging/non-breeding	Early nestling-rearing	Incubation
Number of tracks (individual-years)	Total	148	56	29
	Known nest location	107	50	24
	Known outcome	0	21	12
	Non-breeders	41 (subadults)	16 (winter)	16 (winter)
Breeding season		Nov-Aug (varies with latitude)	Apr-Jul	Apr-Jul
Breeding cycle (days)		110	60	60

Table 2 – Parameter values used to identify nest sites among re-visited locations, chosen by using Classification and Regression Trees (CART) on known nest versus non-nest sites. Values marked with an asterisk were not informed by CART, but were chosen based on data exploration. Consecutive days: maximum number of consecutive days spent at a location. Attendance on top day: percentage of GPS fixes at a location on the day with maximum attendance. Days visited: percentage of days visited between first and last visit.

	Wood stork	Lesser kestrel	Mediterranean gull
Consecutive days (minimum)	14	7	8*
Attendance on top day (minimum)	79%	Unconstrained	26%
Days visited (minimum)	Unconstrained	Unconstrained	Unconstrained

Table 3 – Performance metrics of the nest identification algorithm (see Methods for definitions).

	Wood stork	Lesser kestrel	Mediterranean gull
Positive predictive value	86.24%	100.00%	73.33%
Sensitivity	87.85%	90.00%	91.67%
False negative rate	12.15%	10.00%	8.33%
False positive rate	7.32%	43.75%	0.00%

Figure 1 – Workflow of the analysis to identify nest sites (Part I) and estimate reproductive outcome (Part II) from telemetry data. The R package 'nestR' includes functions to tackle each of the steps depicted in the boxes.

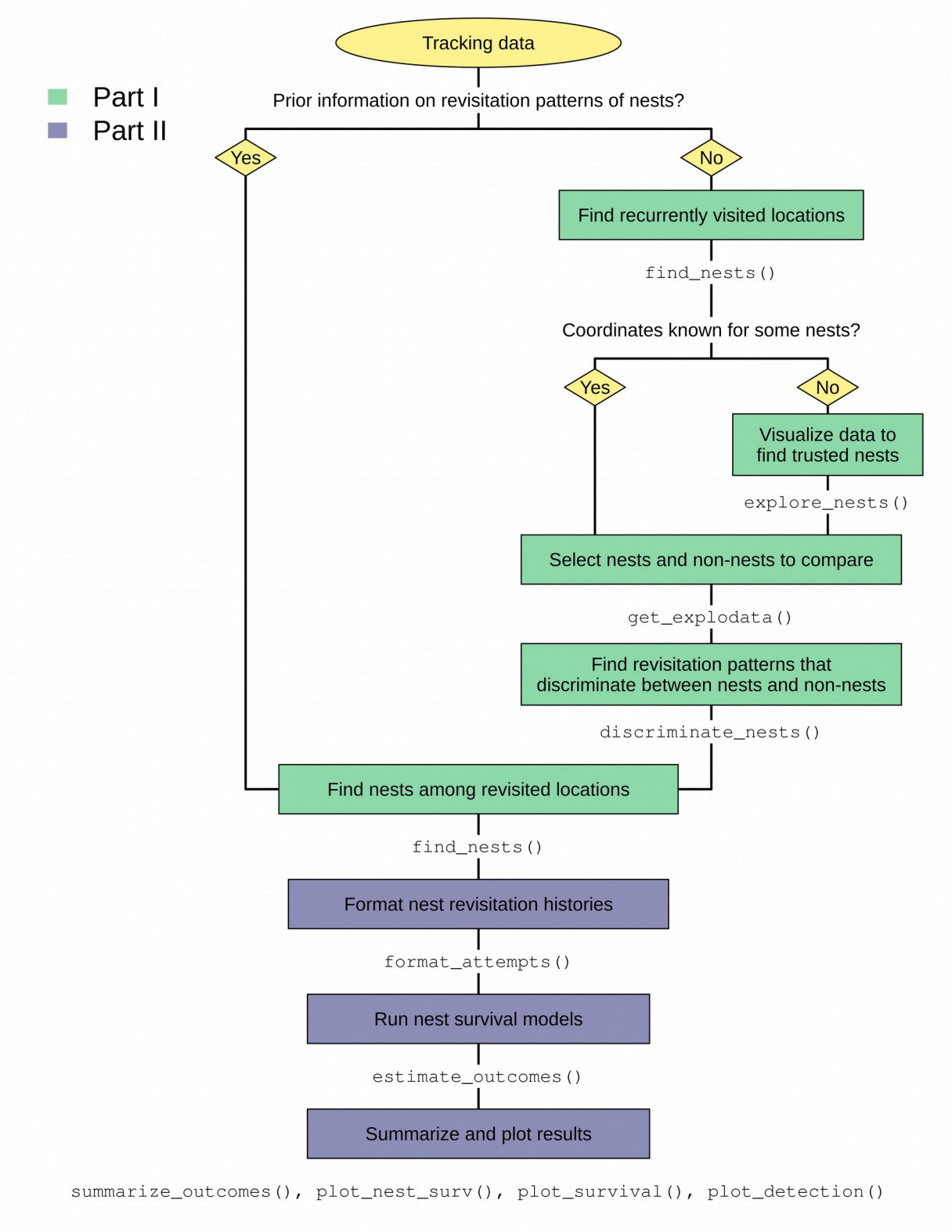

Figure 2 – Output of CART to discriminate nest and non-nest sites in A) wood stork, B) lesser kestrel, C) Mediterranean gull. Within each node (box), the number of known non-nest and nest sites are reported on the left and right, respectively. The root node (top) is recursively split into two until the terminal nodes (bottom). The criterion used to split each node is shown on the corresponding stems (bold font). The label on each node represents the class that was assigned to the content of that node (nest site for “yes” boxes, non-nest site for “no” boxes). Thus, the number on the right in “yes” terminal nodes and the number on the left in “no” terminal nodes correspond to correct classifications, while the number on the left in “yes” terminal nodes and on the right in “no” terminal nodes correspond to incorrect classifications.

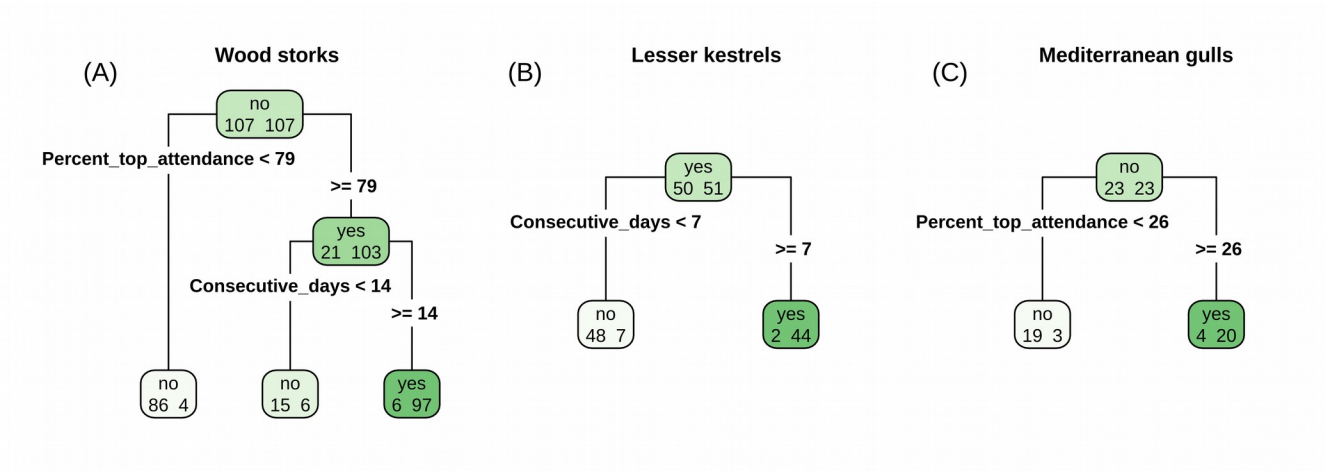

Figure 3 – Probability of visit detection (top row) and survival (bottom row) through time estimated at the population level for A) wood stork, B) lesser kestrel, C) Mediterranean gull. 95% credible intervals are shaded.

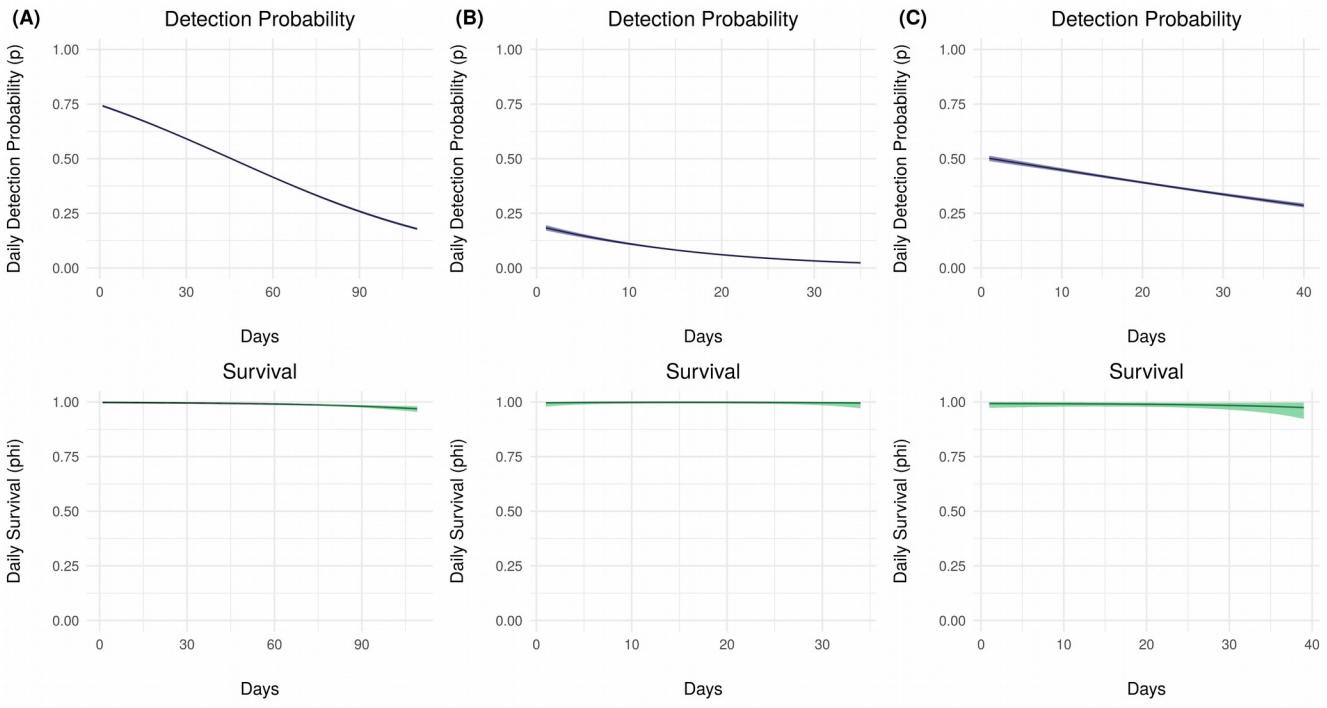
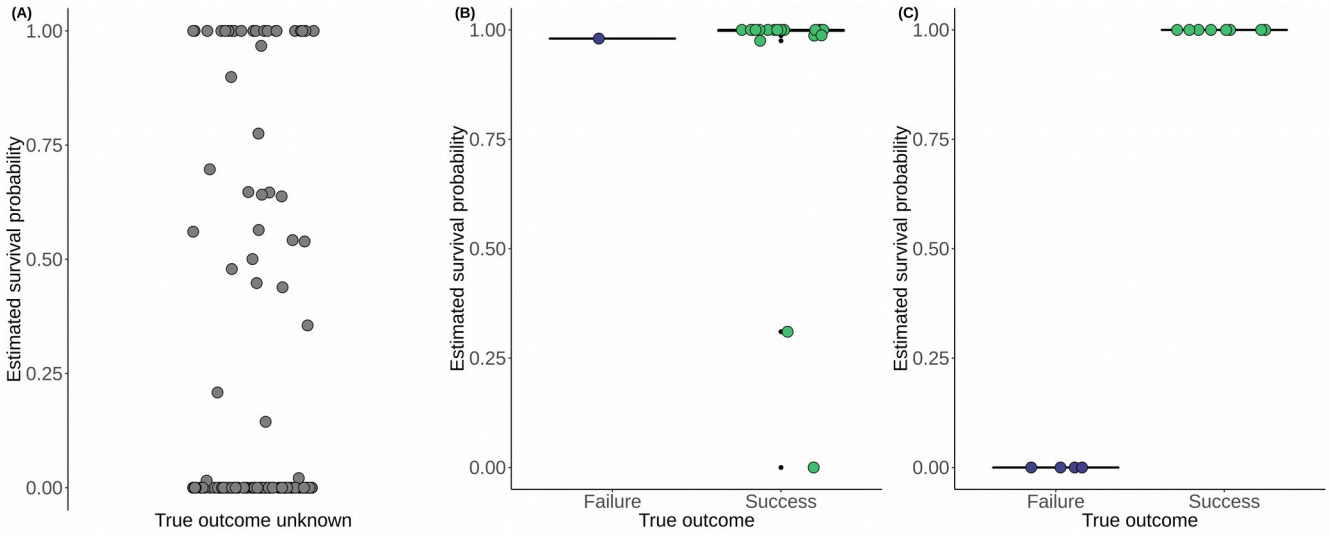
Figure 4 – Estimates of survival probabilities for breeding attempts of A) wood stork, B) lesser kestrel, C) Mediterranean gull. For kestrels and gulls, estimates are plotted in relation to their true outcome. True outcome was unknown for storks. Raw data points are shown as dots (purple for failures, green for successes, gray when true outcome is unknown) overlaid to boxplots (black).