

Does early spring arrival lead to early nesting in a migratory shorebird? Insights from remote tracking

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Advancing breeding phenology is a commonly observed response to climate warming among bird species, potentially in response to shifts in the phenology of key resources. However, for migratory birds breeding at high latitudes, their capacity to breed earlier may be constrained by the time available between arrival on the breeding grounds and nesting, especially for later-arriving individuals. This may have consequences for productivity, as early laying is often linked to higher breeding success, particularly in such seasonal environments. We investigated how migratory arrival timing influences subsequent timing of breeding, in particular whether the time between arrival and laying (arrival–laying gap) varies with arrival date, and if later-arriving individuals are able to catch up with early-arriving conspecifics. We tracked individual Icelandic Black-tailed Godwit *Limosa limosa islandica* with GPS and PTT tags for one to two complete breeding seasons between 2013 and 2022. After arrival in Iceland, most Godwits visited their breeding territory within 5 days, though this interval was longer for earlier-arriving birds. The total gap between arrival and laying was also longer for earlier-arriving birds, such that laying date did not vary significantly with arrival date. These results suggest that, despite individual consistency in migratory phenology, subsequent timing of nesting is probably influenced by other factors, such as mate arrival timing and/or annual variation in environmental conditions. Regular pre-nesting visits to the breeding territory may indicate that Godwits are able to monitor such factors closely and to nest early when conditions allow, but a larger sample of individuals and years is needed to assess whether early-arriving individuals contribute disproportionately to population-level advances in breeding phenology. Widespread tracking with high temporal and spatial resolution helps improve our understanding of phenological variation during the breeding season and its consequences for productivity and variation in juvenile phenology.

Keywords: bio-logging, migration, nest survival, phenology, reproduction.

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Advancing breeding phenology is a commonly observed response to climate warming (Visser & Both 2005, Dunn & Møller 2014, While & Uller 2014)

and, for migratory species, advances in the timing of pre-breeding migratory arrival are also widely reported at the population level (Jonzén *et al.* 2006, Gordo 2007, Parmesan 2007, Knudsen *et al.* 2011, Rakhimberdiev *et al.* 2018). For migratory species that breed in highly seasonal environments, such as at high latitude or altitude, suitable environmental conditions for breeding are present only during a relatively short time window each year (Robinson *et al.* 2009). The period during which these conditions are present is also advancing as a response to climate warming (van Gils *et al.* 2016, Post *et al.* 2018), raising concerns as to whether advances in breeding phenology will be sufficient to continue to exploit them (Møller *et al.* 2008, Both *et al.* 2009, Lameris *et al.* 2018, Kwon *et al.* 2019, Saalfeld *et al.* 2021).

For example, many migratory waders breed at high latitudes, where their capacity to breed earlier is likely to be constrained by arrival date and the time required between arrival and nesting (Gill *et al.* 2014). In such species, breeding phenology can be influenced by the environmental conditions experienced during this period, such as temperature (Alves *et al.* 2019, Meltofte *et al.* 2021), snow cover (Meltofte *et al.* 2007, Mortensen *et al.* 2016), vegetation growth (Laidlaw *et al.* 2020) and available food resources (Meltofte *et al.* 2007, Mortensen *et al.* 2016, Zhemchuzhnikov *et al.* 2021, Lameris *et al.* 2022; but see Verhoeven *et al.* 2022), as well as the timing of arrival of the mate (Gunnarsson *et al.* 2004).

As the timing of spring arrival of many migratory wader populations is advancing (Gunnarsson & Tómasson 2011, Rakhimberdiev *et al.* 2018), the time available between the arrival of individuals and the occurrence of suitable conditions at their breeding sites may constrain their ability to nest earlier (Gunnarsson 2010, Lourenço *et al.* 2011, Meltofte *et al.* 2018, Carneiro *et al.* 2019). Therefore, understanding the links between timing of migration (arrival dates) and timing of breeding (laying dates) can help to reveal whether advances in breeding phenology are likely to be concentrated among early-arriving individuals.

Early arrival in migratory birds is often linked to higher breeding success and productivity (Smith & Moore 2004, Costa *et al.* 2021), as earlier-breeding individuals often enjoy higher nest survival (Kentie *et al.* 2015) and have more time to re-lay following nest loss (Halupka & Halupka 2017, Morrison *et al.* 2019, Méndez *et al.* 2022). Early laying can

also lead to early hatching (Alves *et al.* 2019), and earlier-hatching chicks often achieve faster growth rates (Lameris *et al.* 2022) and higher rates of recruitment into the breeding population (Kentie *et al.* 2018, Alves *et al.* 2019, Saalfeld *et al.* 2021, Nightingale 2022). However, earlier arrival does not necessarily lead to earlier breeding (Lourenço *et al.* 2011, Merkel *et al.* 2019).

The advantages of early breeding raise the question as to why advancing breeding phenology is not more widely observed in migrants, especially if trophic mismatches between the timing of breeding and subsequent food resource peaks are becoming more common (Robinson *et al.* 2009, Lameris *et al.* 2022; but see Zhemchuzhnikov *et al.* 2021). Migrating early to facilitate earlier breeding may be risky, with risks including increased energy requirements of experiencing harsh environmental conditions (Senner *et al.* 2015, Alves *et al.* 2016). In addition, opportunities to advance breeding phenology may be constrained by the length of the arrival–laying gap: earlier-arriving individuals may need to wait longer for suitable conditions on the breeding grounds or for the arrival of a mate, or require more time to restore body condition after a harsher migration (particularly in income breeders such as waders; Klaassen *et al.* 2001), which may be more common early in the migratory period. If the arrival–laying gap is longer for early-arriving individuals, then when such constraints are lessened, e.g. through climatic amelioration (Schroeder *et al.* 2012), the early-arriving subset of the population would have greater potential to advance phenology than other individuals. Exploring the links between the arrival–laying gap and breeding phenology requires a study system in which timings of migration and breeding vary sufficiently to generate variation in the arrival–laying gap, and in which the timings of individuals can be tracked.

The Icelandic Black-tailed Godwit *Limosa limosa islandica* (hereafter, Godwit) is a long-distance migratory wader that breeds in lowland Iceland and winters on the west coast of Europe (Gunnarsson *et al.* 2005). Arrival in Iceland typically occurs from mid-April to mid-May, and laying from mid-May to mid-June (Gill *et al.* 2014, Alves *et al.* 2019). Substantial phenological variation has been demonstrated in this well-studied population. Timing of spring arrival in Iceland has advanced significantly (Gunnarsson & Tómasson 2011, Gill *et al.* 2014), a trend linked to an increased frequency of early-arriving

individuals among new recruits (Gill *et al.* 2014, 2019). Godwits also show earlier laying, hatching and fledging in warmer years (Alves *et al.* 2019), and warmer years also have higher productivity (Gunnarsson *et al.* 2017). Across all wader species that breed in Iceland, those that show advancing arrival dates have a longer gap between arrival and laying (Gunnarsson 2010, Gill *et al.* 2014, Carneiro *et al.* 2019), suggesting that this period may play a role in facilitating phenological shifts. A better understanding of the causes and consequences of variation in the arrival–laying gap is therefore extremely important, as it is during this period that Godwits and other migrants may be most flexible in terms of responding to environmental change. However, the intra-individual relationships between the sequential timings of successive breeding-season events (e.g. arrival, establishing a territory and laying) remain unexplored at the sub-arctic latitudes of Iceland.

In this study, we use data from Icelandic Godwits tracked with GPS/PTT tags to explore the individual-level variation in laying phenology cascading from the timing of arrival of the first visit to the breeding territory, and to subsequent laying/re-laying dates. We first quantify the length of the arrival–laying gap and how it varies among individuals breeding across Iceland. We then test whether earlier-arriving birds have longer arrival–laying gaps, higher hatching success and higher propensity to re-nest. Finally, we explore the extent to which arrival and breeding dates, and the gaps between them, are consistent for individuals tracked for more than 1 year.

METHODS

Captures and tagging

Between 2013 and 2021, eight individual Icelandic Black-tailed Godwits were caught at non-breeding sites (Iberia) or breeding sites (Iceland) and fitted with satellite tracking tags (Table 1). Of these, five birds were fitted with 9.5-g PTT-100 tags from Microwave Technology: two birds were nest-trapped in Iceland while breeding during the 2015 season, and three were captured during winter/spring. In most cases ($n = 4$), PTT tags were programmed to switch off for 48 h to conserve battery power, before transmitting for 10 h (Senner *et al.* 2019; Table 1). Three further birds were

mist-netted in Portugal during winter of 2020–2021 and fitted with 4.5-g GPS/GSM tags from HQXS. These tags were programmed to transmit every 6 ($n = 1$) or 8 h ($n = 2$; Table 1). All birds were sexed after capture using biometrics (Gunnarsson *et al.* 2006).

From each tag, we extracted all position data within Iceland, resulting in one ($n = 3$ individuals), two ($n = 4$ individuals) or four ($n = 1$ individual) complete breeding seasons in Iceland, defined as the time when both arrival and departure were recorded. This resulted in a total of 13 breeding seasons from eight individuals.

To investigate how migratory arrival timing influences breeding phenology, we identified three key dates in the breeding season (Fig. 1):

- Arrival: the first day of the year in which the individual was located in Iceland.
- First-visit: the first day on which the individual visited the 200-m buffer around the nest location (see *Nest locations and timing* below) in which it bred later in the season (for birds that made multiple nesting attempts, we used the location of the first nest to estimate this variable).
- Laying: the day on which the first egg of the nesting attempt was laid (for birds that made multiple nesting attempts, again we considered the first nesting attempt).

We also consider three gaps between these dates: arrival–laying and two subdivisions of it: *arrival-(first-)visit* and *(first-)visit-laying* (Fig. 1). In all analyses we use Julian dates adjusted for leap years.

Previous analyses suggest that tag effects on reproduction are limited to tags attached to a neck collar, rather than the leg-loop attachments used for the tags in this study (Bodey *et al.* 2018). We confirmed that timing of breeding of tagged individuals is similar to that of untagged birds (see below).

Data-cleaning and sub-setting

To reduce the error associated with locations from PTT tags, we followed the data-cleaning procedure in Chan *et al.* (2019), omitting low-quality fixes (classes 0, A, B and Z). We also calculated the implied speed of movement by dividing the great circle distance between successive locations by the

Table 1. Capture, marking and tag information for the eight individual Icelandic Black-tailed Godwits tagged in Iceland (IS), Portugal (PT) and Spain (ES) whose arrival at and breeding in Iceland were analysed in this study.

Individual	Marking				Transmissions			Locations		
	Date ^a	Location	Sex	Tag type	First	Last	Days	All	Iceland	Schedule (h)
Barreiro	12/11/20	Tagus Estuary, PT	M	GPS	12/11/20	17/07/22	612	2363	530	8
Tejo	12/11/20	Tagus Estuary, PT	M	GPS	13/11/20	10/07/22	604	2204	444	8
Mouchão	11/03/21	Tagus Estuary, PT	F	GPS	03/11/20	15/07/22	619	1003	130	6
Kaldadarnes	18/06/15	Kaldaðarnes, IS	F	PTT	18/06/15	10/12/18	1271	3608	793	10 on; 48 off
Rotterdam	06/02/13	Badajoz, ES	F	PTT	06/02/13	17/04/15	800	3560	791	10 on; 48 off
Sarilhos	09/01/19	Tagus Estuary, PT	F	PTT	09/01/19	–	–	14 860	1968	Constant
Tims	09/02/14	Badajoz, ES	F	PTT	09/02/14	28/08/15	566	1738	195	10 on; 48 off
Vorsaber	27/06/15	Vorsabær, IS	F	PTT	27/06/15	13/02/17	597	1938	413	on; 48 off

Transmission from Sarilhos is ongoing, so no last transmission is reported. Schedule indicates the frequency with which locations are recorded (GPS tags) or hours during which they are recorded ('on') vs. not recorded to save battery ('off'). ^aDates are given as day/month/year.

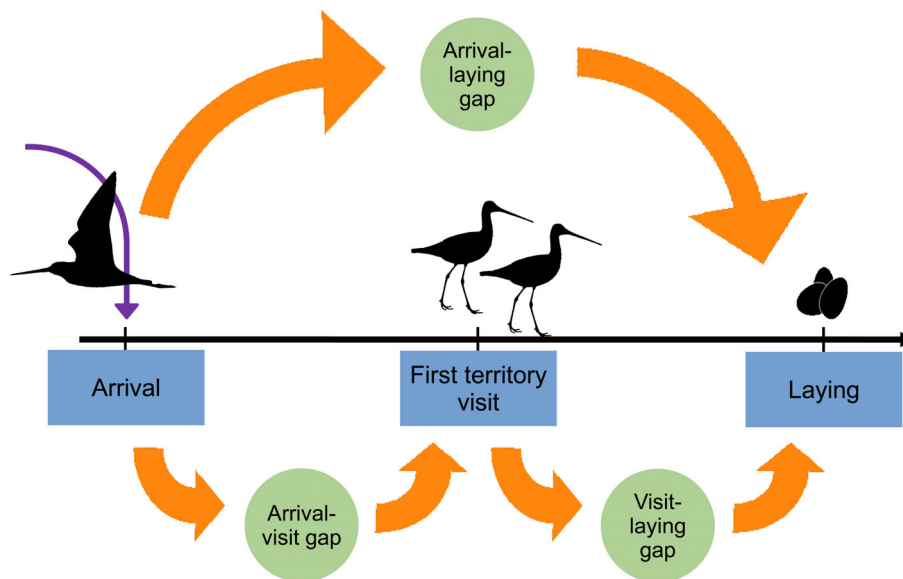


Figure 1. Key events (blue rectangles) during the early breeding season of the Icelandic Black-tailed Godwit, and the time gaps between them (green circles). (1) Arrival in Iceland from the non-breeding grounds. (2) First visiting the territory and forming a pair. (3) Laying a clutch of eggs. The total arrival–laying gap duration can be considered as the sum of two shorter gaps: one between arrival and the first territory visit, and a second between the first territory visit and laying.

time elapsed between those fixes; locations implying a speed ≥ 120 km/h were considered erroneous, as such a speed is above the maximum sustainable rate of movement (Douglas *et al.* 2012). All locations from GPS tags had an error ≤ 20 m.

Nest locations and timing

To identify nest locations and thus the timing of related events, we used the R package `nestR`

(Picardi *et al.* 2020) for R (R Core Team 2022) to analyse recursive movements for each tagged bird in each year (hereafter, 'bird-year'). We defined the breeding season conservatively as extending between 1 May and 31 July (Gill *et al.* 2014), and the nesting cycle as lasting 23 days (Alves *et al.* 2019). We then used the `find_nests()` function to identify locations repeatedly revisited during this period. For this analysis we used a buffer of 200 m around each point to account for

uncertainty in tag locations, except for the individual Sarilhos, which required a buffer of 300 m to detect any nests, possibly due to the constant transmission schedule lowering battery levels and thus the accuracy of satellite fixes. Exploratory analysis suggested that the method used was not sensitive to the size of buffer, with values in the range 200–500 m producing very similar estimates of locations and timings.

The `find_nests()` method distinguishes nest locations from other revisited locations (e.g. frequently used foraging sites) using a set of frequency-based metrics: the maximum number of consecutive days a location is visited, the proportion of days it is visited between the first and last visit, and the minimum number of fixes required on a given day for it to be included in the above calculations (Picardi *et al.* 2020). All of these values are expected to be higher for nests than other revisited locations at the chosen spatial scale of the buffer. We defined different minimum acceptable criteria for GPS and PTT tags, as PTT tags had lower spatial accuracy and regular 48-h periods without transmission, imposing a limit on the number of consecutive days at a location that could be observed (*consecutive days*: GPS 5, PTT 2; *proportion of days*: GPS 0.5, PTT 0.25). Putative locations that overlapped in space and time were discarded, retaining only the location that maximized the above parameters.

For the two individuals that were caught on the nest in Iceland (Table 1), actual nest locations in the year of capture were compared with the estimated nest locations in subsequent years produced by `nestR` by calculating the geodesic distance separating them using the `dism()` function of the `geosphere` package (Hijmans *et al.* 2017). We used the same approach to determine the distance from the nest location of each point recorded during the nesting attempt, in order to calculate the 95% kernel as an estimate of breeding territory size. Having identified the nesting location for each bird in each year, the initiation of laying is estimated within `nestR` by assuming that the start of the longest series of consecutive days when the location was revisited corresponds to the beginning of the nesting attempt, as attendance is highest during this period (Picardi *et al.* 2020). For nests that survived long enough to hatch successfully, the end of the nesting attempt is considered to be 23 days after initiation (Alves *et al.* 2019); for nests that failed, the

end of the attempt was the last visit to the nesting location.

Event timing and gap length

To explore the sequential relationships between the dates of key events and the duration of gaps between them we used structural equation modelling (SEM; Laughlin & Grace 2019). In this approach, individual relationships are modelled and then assembled in a causal probabilistic network (Grace *et al.* 2012). Thus, indirect effects can be modelled explicitly (Laughlin & Grace 2019), such as temporal dependencies in the annual schedule of migratory birds (e.g. Carneiro *et al.* 2022). To this end, we modelled relationships between events and gaps using five linear relationships (Table 2) jointly within an SEM approach.

The SEM was fit in a Bayesian framework using the `brms` package (Bürkner 2017) for R (R Core Team 2022). We ran three chains for 25 000 iterations, of which 20 000 were discarded as warm-up, retaining 5000 samples per chain (15 000 total) for inference. Default settings were generally used, except that `adapt_delta` was set to 0.99 and we set a weakly regularizing prior of $\sim N(0, 1)$ on each beta coefficient to avoid overfitting and improve convergence (McElreath 2020). We assessed model fit and convergence in three ways: visually through inspection of traceplots; by ensuring that $Rhat$ was ≤ 1.01 for each estimate (Brooks & Gelman 1998); and by ensuring that Pareto k diagnostics were < 0.7 for all observations (Veh-tari *et al.* 2017).

Hatching success: nest survival and re-nesting

To estimate daily nest survival probability and how it varies according to arrival date, laying date and the length of the arrival–laying gap, we fitted a Bayesian hierarchical model using the location data. This model, analogous to a Cormack–Jolly–Seber capture–mark–recapture model, considers each transmitted location as an observation event with a probability P of detecting the bird at the nest location. These observations are used to estimate the (latent) survival status of each nest and thus the underlying daily survival probability ϕ . Our model was based on the null (constant survival, constant detection) model in `nestR`

Table 2. The five relations combined in a structural equation model (SEM) to explore the relationship between arrival date and the timings of other breeding-season events and gaps.

Response	Error structure	Predictor	Estimate	se	Credible intervals	
					Lower	Upper
Arrival–visit gap	Poisson	Intercept	11.85	1.64	8.67	15.11
		Arrival date	−0.08	0.01	−0.11	−0.05
Visit–laying gap	Poisson	Intercept	1.88	1.57	−1.20	4.96
		Visit date	0.00	0.01	−0.02	0.03
Arrival–laying gap	Poisson	Intercept	6.61	0.92	4.79	8.44
		Arrival date	−0.03	0.01	−0.04	−0.02
Visit date	Normal	Intercept	60.94	19.75	21.69	100.94
		Arrival date	0.57	0.15	0.26	0.87
Laying date	Normal	Intercept	28.18	57.13	−80.98	144.75
		Arrival date	0.04	0.44	−0.81	0.91
		Visit date	0.83	0.57	−0.31	1.91

For each relationship we present the response variable, error structure, predictor variables and path coefficients from the SEM (with significant relationships in **bold**). Analyses where the response variable was a gap had a Poisson error structure, whereas when the response variable was a (Julian) date, Normal error structure was used. Each estimate is presented with its standard error (se) and 95% credible intervals.

(Picardi *et al.* 2020), but was adapted in two ways: (1) the probability of detection P was allowed to differ between the two tag types (GPS vs. PTT) and (2) daily nest survival φ_i was modelled as a function of the arrival date (A), laying date (L) and arrival–laying gap (G) associated with each individual/nest:

$$\text{logit}(\varphi_i) = \beta_0 + \beta_1 \times A_i + \beta_2 \times L_i + \beta_3 \times G_i.$$

All priors were drawn from the Normal distribution, and are given below in the format $\sim N$ (mean, sd). We set an informative prior on daily nest survival of $\text{logit}(\varphi) \sim N(3, 0.4)$, approximately equivalent to $\varphi \sim N(0.95, 0.02)$ on the logit scale, as previous work indicated that 50–75% of nests successfully hatch (Gill *et al.* 2007), which translates to 0.97–0.99 daily survival over the 23-day nesting cycle used in these analyses. Detection probability was given a weakly informative prior of $\text{logit}(P) \sim N(0, 1)$, approximately equivalent to $P \sim N(0.5, 0.2)$ on the logit scale, in order to avoid extreme values. The β parameters for arrival date, laying date and tag type were all given regularizing priors of $\beta_i \sim N(0, 0.1)$ to avoid overfitting (McElreath 2020).

We used three chains to assess convergence and mixing. Initial checking included visual inspection of trace plots to assess convergence, mixing and stability of density plots for each parameter's

posterior distribution to ensure they were unimodal, and that the $Rhat$ statistic (Brooks & Gelman 1998) was ≤ 1.01 . The first 2000 iterations were discarded as burn-in to allow the model to reach a stable distribution (as assessed by examining traceplots and plots of running means), followed by 20 000 sampling iterations for inference. These samples were thinned to every 5th iteration to reduce autocorrelation, leaving a total of 4000 samples per chain (12 000 total) for inference. This analysis was conducted using JAGS (Plummer 2003) via the R package rjags (Plummer *et al.* 2016).

Using this model, we calculated for each nest the probability of successful hatching, i.e. the probability that the attempt survived the full 23-day nesting cycle; and the duration of the attempt, i.e. the number of days for which the nest was actively revisited by the adult. Mean estimates are reported with their 95% credible (highest posterior density) intervals (CIs).

Where multiple nesting attempts by an individual within a year were identified, we considered subsequent attempts to represent re-nesting. To determine whether re-nesting was more likely after an unsuccessful or a successful attempt, we compared nests that were followed by re-nesting with those that were not in terms of their probability of success, using a generalized linear model (GLM) with a binomial error structure and log link

functions, with estimated survival probability (derived from the survival model described earlier) as the response and subsequent re-nesting status ('re-nesting' or 'not re-nesting') as a (binary) predictor. We also compared the duration of nesting attempts that were followed by re-nesting or not (independent of the hatching success of the first clutch) using a Welch's *t*-test.

Finally, to determine whether timing of arrival or laying, or the length of the gap between them, influenced the probability of re-nesting, we compared nests followed by re-nesting or not in terms of (1) adult arrival date, (2) laying date (of original clutch), (3) length of arrival–laying gap and (4) last date of the original attempt, also using Welch's *t*-tests.

To calculate the distance between subsequent nesting attempts by the same individual in the same year (i.e. re-nesting), we again calculated the geodesic distance between them using the `dism()` function of the R package `geosphere` (Hijmans *et al.* 2017).

RESULTS

Nest locations and timings

We identified 23 nesting attempts by eight individuals between 2013 and 2022 (Table 3), distributed across south, west and northeast Iceland (Fig. 2). Of the 13 individual breeding seasons in our sample, six (46%) included a sole nesting attempt, four (31%) included two attempts and three (23%) included three attempts (Table 3). No nests could be identified for one individual (Sarilhos) during the last 2 years of study (2021–2022) due to the scarcity of location data transmitted from the tag (Supporting Information Appendix S1) and these years for this individual were therefore excluded from the analyses.

There was considerable between-individual variation in the timings of Godwits (Fig. 3). Godwits in this sample arrived in Iceland between 21 April and 28 May, with a median arrival date of 7 May. First-visits to breeding territories were made between 5 and 31 May, with a median first-visit date of 12 May. Laying of first clutches occurred between 9 May and 18 June, with a median of 23 May. Re-nesting overlapped considerably with first clutches, with the earliest occurring on 22 May and the latest on 15 July. Thus, the earliest-nesting Godwits had begun laying when approximately

Table 3. Number of nesting attempts by each individual in each year.

Individual	Year	<i>n</i>
Barreiro	2021	1
Barreiro	2022	2
Kaldadarnes	2017	1
Kaldadarnes	2018	2
Mouchão	2021	3
Rotterdam	2013	1
Rotterdam	2014	1
Sarilhos	2019	2
Sarilhos	2020	3
Tejo	2021	1
Tejo	2022	2
Tirns	2015	3
Vorsaber	2016	1

half the individuals in this sample were yet to arrive in Iceland, and 67% of first attempts were laid before the latest bird arrived. The earliest re-nesting event also occurred before the two latest birds had arrived (Fig. 3).

The four estimated nest locations for the two individuals nest-trapped in Iceland were all ≤ 4 km of the original nest locations where these birds had been ringed in previous years (mean 2.8 ± 0.4 se km), distances smaller than the distance moved during nesting (3.3–33 km; Table 4). The distribution of estimated nest dates was also similar to known nest dates derived from field studies (Supporting Information Appendix S2).

The SEM fit the data well (all Pareto $k < 0.7$) and showed several pathways by which arrival date influences subsequent timings (Fig. 4; Table 2). Earlier-arriving Godwits made their first visit to the breeding territory earlier (Fig. 5a), but had longer arrival–visit gaps (Fig. 5b). There was no correlation between the date of first visit and laying date, or the length of the visit–laying gap (Fig. 5c,d). Although arrival date did not predict laying date (Fig. 5e), the arrival–laying gap was shorter for later-arriving birds (Fig. 5f; Table 2). Repeating this analysis including only the first tracked breeding season of each individual resulted in qualitatively similar results (Supporting Information Appendix S3).

Nest survival and re-nesting attempts

The nest survival model converged well (all $Rhat = 1$) and produced informative posterior

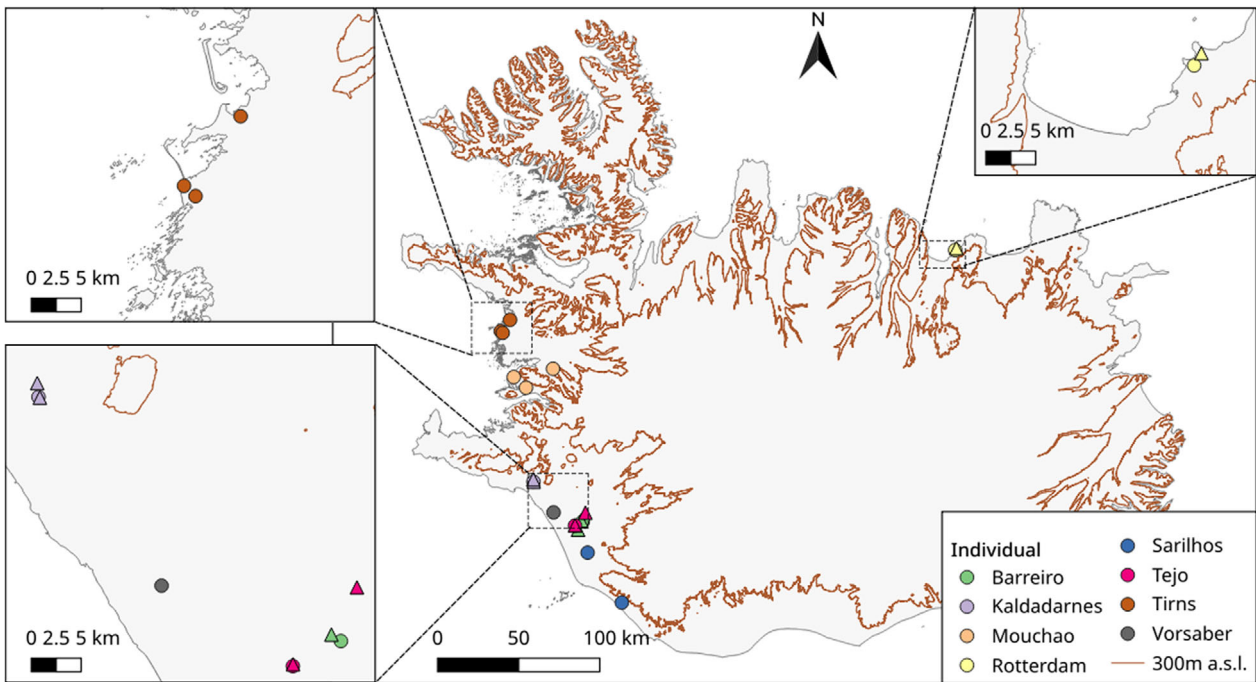


Figure 2. Locations of each nesting attempt of tracked Icelandic Black-tailed Godwits in Iceland, estimated from remote tracking data. Each individual is plotted with a distinct colour, and where individuals were tracked for multiple years the second year is represented with a triangle. Brown lines indicate the 300 m above sea level contour, below which most Icelandic Godwits breed.

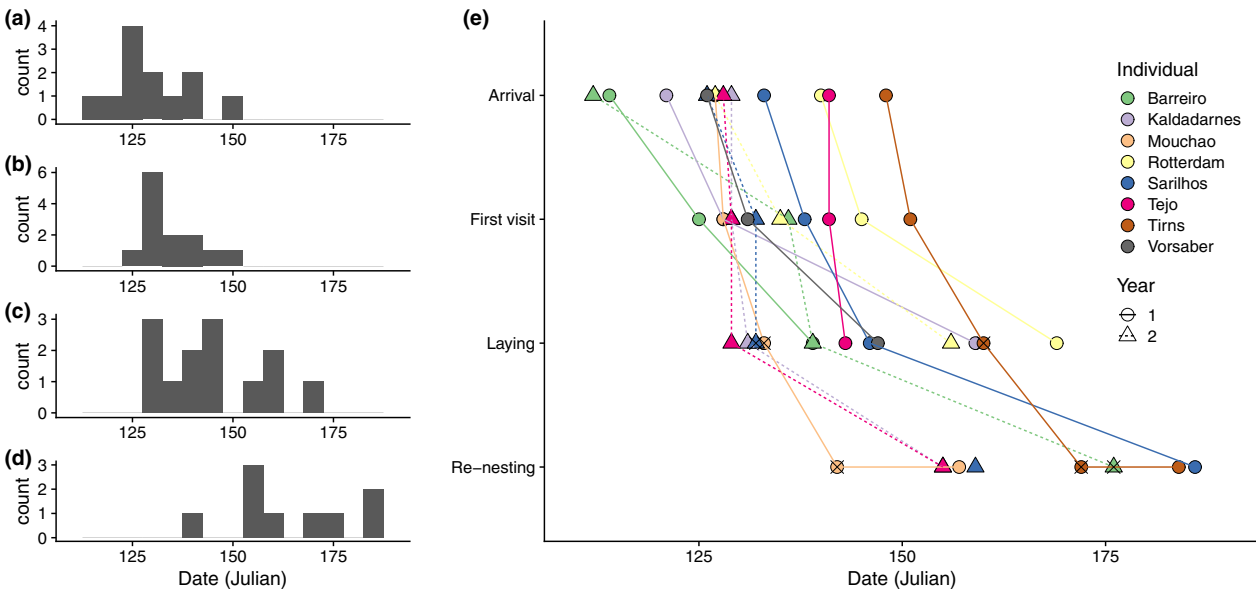
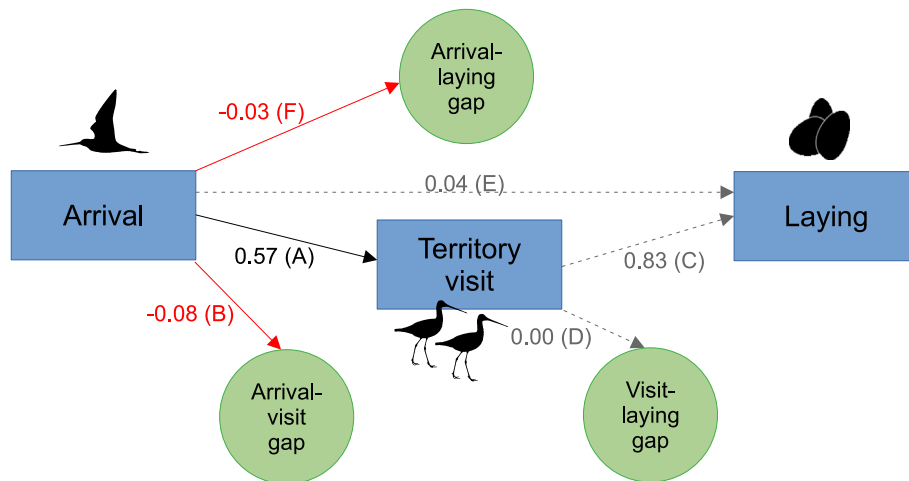


Figure 3. Individual variation in the breeding-season timings of eight Icelandic Black-tailed Godwits tracked between 2013 and 2022. Left column: variation in (a) arrival dates in Iceland; (b) first detections at the breeding territory (first territory visit); (c) beginning of first nesting attempt (laying date); and (d) re-nesting attempt. Right column: (e) individual-level variation in the progression from arrival (in Iceland) to the first visit to territory, first and re-nesting attempts. Nests that did not hatch successfully are indicated with a crossed-out symbol e.g. ⊗. For individuals tracked in two breeding seasons, the second year is shown with a triangle. Data from the same bird-year are connected with solid (first year of tracking) or dashed (second year of tracking) lines.

Table 4. Distance between known nest locations of two Black-tailed Godwits captured and tagged on the nest in Iceland (in 2015), and estimated locations generated from tag data collected during subsequent breeding seasons.

Individual	Capture			Estimates			Distance (km)	Territory radius (km)
	Year	Lat	Lon	Year	Lat	Lon		
Kaldaðarnes	2015	63°55'42.6"	-21°9'37.9"	2017	63°56'42.0"	-21°11'49.2"	2.57	2.52
				2018	63°56'42.0"	-21°11'38.4"	2.47	2.73
				2018	63°57'21.6"	-21°12'39.6"	3.94	4.84
Vorsabær	2015	63°50'30.4"	-20°51'16.5"	2016	63°50'2.4"	-20°48'36.0"	2.36	3.05

**Figure 4.** Network diagram of the SEM showing the correlations between timing of events (blue rectangles) and the length of gaps between them (green circles) during the breeding season of Icelandic Black-tailed Godwits. Significant correlations are shown with solid arrows (black for positive and red for negative), whereas non-significant relationships are shown with grey dashed arrows. Numbers next to arrows indicate the coefficient for the correlations, and letters beside it link to plots on Figure 5.

estimates that were not unduly influenced by priors (Supporting Information Appendix S4). Daily nest survival was estimated to be 0.97 (95% credible interval (CI) 0.96–0.98). The probability of detecting a bird at the nesting location was significantly higher using GPS tags ($P = 0.59$; 95% CI 0.54–0.63) than PTT tags ($P = 0.16$; 95% CI 0.14–0.17). Nest survival rate did not vary significantly with arrival date ($\beta_1 = -0.04$; 95% CI -0.53 to 0.48), laying date ($\beta_2 = -0.02$; 95% CI -0.53 to 0.48) or arrival-laying gap ($\beta_3 = 0.001$; 95% CI -0.49 to 0.52).

The nest survival model indicated that, of the 23 nesting attempts identified, 13 (57%) were highly likely to have succeeded (i.e. a probability of hatching > 90%) and six (23%) were highly likely to have failed (probability of hatching < 10%). The remaining four had

probabilities of success of 12.5%, 65.0%, 66.3% and 82.5%, representing a probable failure, two unknown outcomes and a probable success, respectively. Hatching success in this sample was therefore ~60–75%. Nests that probably failed (probability of success < 10%) did so after a mean of 10.2 ± 1.6 days (range 6–15).

Of the 10 re-nesting attempts, six (60%) occurred within 7 days following the end of the previous attempt (median 5.5, range 2–18). Nesting attempts that were followed by re-nesting and those that were not did not differ significantly in terms of the arrival date of the adult ($t_{19,0} = -0.4$; $P = 0.7$), lay date of original attempt ($t_{18,8} = -0.4$; $P = 0.7$), failure date of original attempt ($t_{16,0} = -0.4$; $P = 0.6$), arrival-laying gap length ($t_{20,1} = 0.2$; $P = 0.8$), first breeding attempt duration ($t_{19,9} = 0.03$; $P = 0.97$) or the estimated

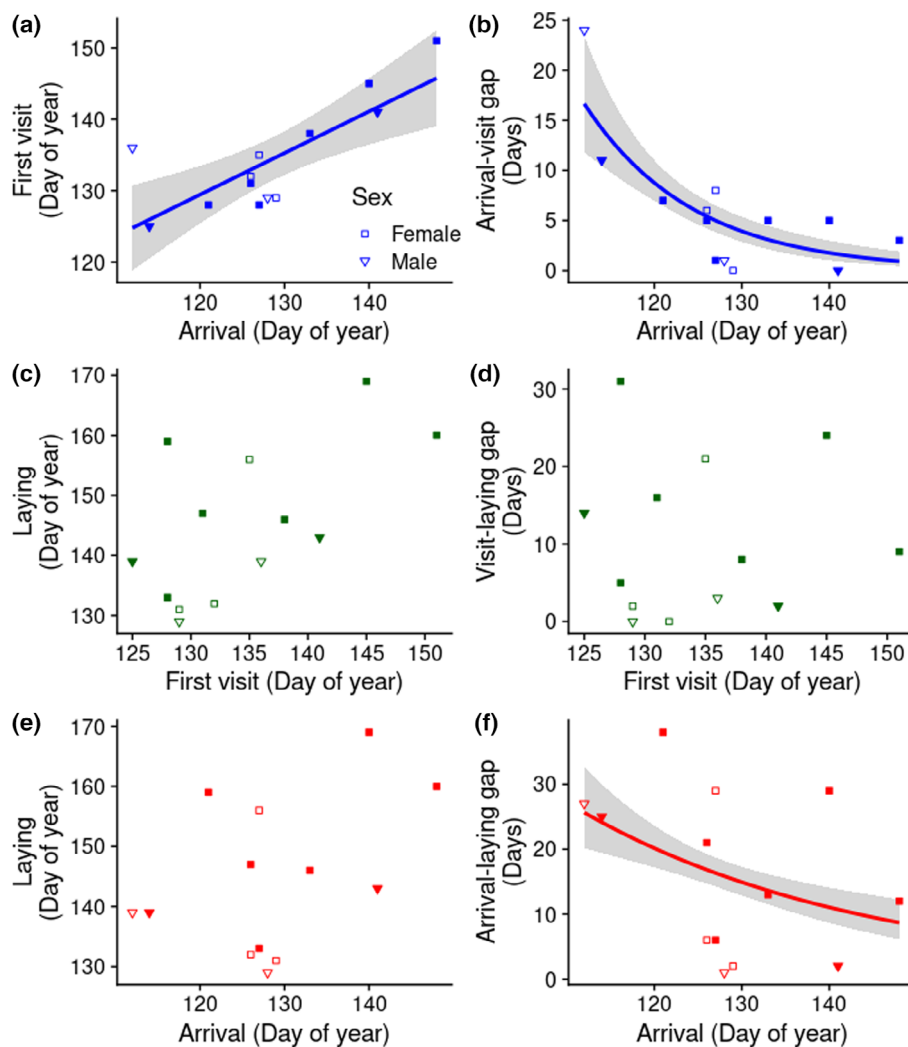


Figure 5. Individual paths from the SEM predicting how dates of events influence dates of subsequent events (left column): (a) first visit with arrival date, (c) laying date with first visit date and (e) laying date with arrival date; and the length of gaps (right column): (b) arrival–visit gap with arrival date, (d) arrival–laying gap with first-visit date and (f) visit–laying gap with arrival date; during the breeding seasons of eight tracked Icelandic Black-tailed Godwits. Males are shown with inverted triangles and females with squares. Unfilled shapes represent the second year an individual was tracked. Fits where confidence intervals excluded zero are shown with their 95% credible intervals (shaded area).

probability that the first clutch hatched successfully, according to the nest survival model above ($\text{logit}(y) = 0.7 - 0.03x$; $P = 0.9$). Re-nesting locations were between 1.5 and 37.4 km from that individual's first nesting location that year, with a mean distance (\pm se) of 12.1 ± 3.5 km.

Individual consistency

Individuals' arrival dates differed slightly between years (mean 9 ± 2.1 se days) but this variation was small compared with the total population

variation (21 April–28 May; Fig. 6a). Timing of first territory visit varied similarly (8.0 ± 2.0), though the range of dates in the sample was lower (5–31 May; Fig. 6b). The largest individual variation was recorded with laying date (13.8 ± 4.4 days; range 9 May–18 June; Fig. 6c).

DISCUSSION

We tracked eight Black-tailed Godwits for 13 complete individual breeding seasons and 23 nesting attempts in Iceland. We found considerable

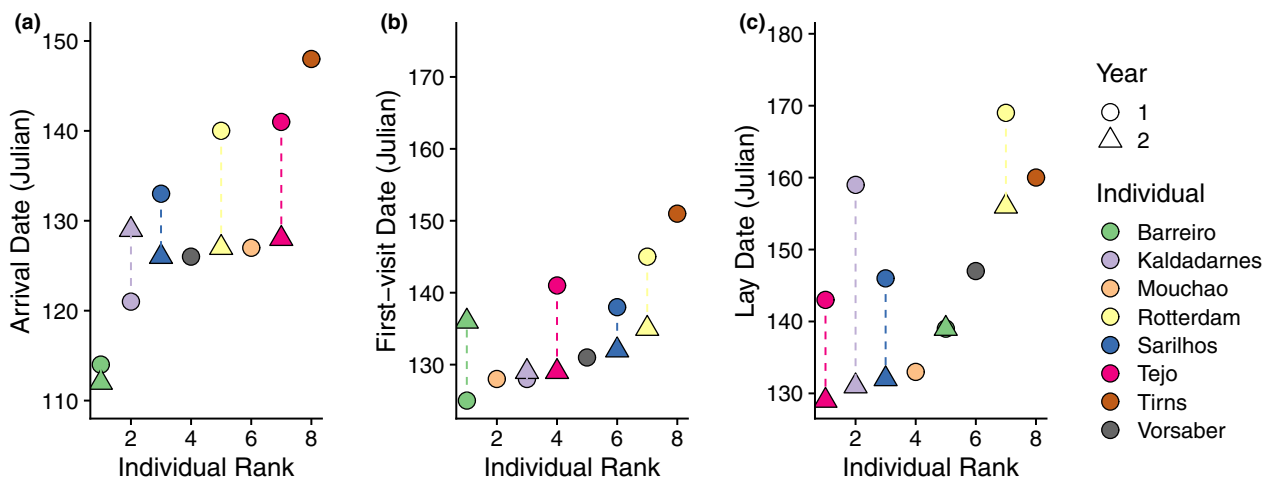


Figure 6. Individual consistency in the timing of (a) arrival, (b) first-visit to the breeding territory and (c) laying, recorded in eight Icelandic Black-tailed Godwits. Individuals are ordered from earliest to latest (left to right) within each plot and where individuals were tracked for 2 years, the earliest value was used as reference. Dates from the second year of tracking are shown with triangles, and data from the same individual in multiple seasons are connected with dashed lines. The y-axis of each plot has an equal range of 50 days to facilitate comparisons.

between-individual variation in timings, with the earliest-laying individuals doing so before later individuals had reached Iceland. Early-arriving Godwits visit their territory sooner in the season than later-arriving individuals, despite having a longer arrival–visit gap. The total arrival–laying gap was also longer for early-arriving birds. On the other hand, we did not find evidence that early-arrivers or early first-visitors had earlier lay dates, nor did we find a link between arrival or first-visit date and the length of the visit–laying gap. While some birds lay before others arrive, those very early layers are not necessarily the earliest arrivers, hence the lack of correlation (Fig. 3). There was no significant correlation between arrival date and nest survival, which was high throughout the season, and re-nesting occurred in both early- and later-arriving or laying individuals. Furthermore, re-nesting occurred after nesting attempts that apparently failed both during the clutch stage, and after attempts that apparently hatched successfully (but probably following failure at the chick stage). The lack of long gaps (≥ 21 days; Alves *et al.* 2019) between successive nesting attempts suggests no evidence for re-nesting after successful fledging.

We found that Godwits may visit their future nesting location several days or weeks before laying, with earlier-arriving individuals making earlier first-visits, and the arrival–visit gap being shorter

for later-arrivers. These pre-laying visits may facilitate assessment of environmental conditions on the territory and their suitability for breeding (van den Brink *et al.* 2008). Alternatively, they might represent a rendezvous with the previous season's mate. Paired Godwits do not winter together, or meet each other in migratory flocks on arrival in Iceland, but rather arrive synchronously on the breeding grounds, typically within ~ 3 days of each other, with divorces typically occurring when a male arrives later than the female (Gunnarsson *et al.* 2004; similar results are reported for Dutch Godwits by Lourenço *et al.* 2011). In such cases, re-pairing must occur, which is likely to delay laying. Unfortunately, in this dataset we do not know when mates visited the territory. Synchronous arrival in a place determined during the previous breeding season might be a simple but effective mechanism to facilitate mate fidelity in populations which have low migratory connectivity between breeding and wintering sites (Kokko *et al.* 2006). Such a mechanism may also lead to assortative mating between birds on similar schedules.

We did not find a strong relation between arrival and laying dates in this sample, though later-arriving birds have shorter arrival–laying gaps. Although the sample of tracked birds available for this study was relatively small, our results echo those previously reported for Godwits breeding

elsewhere. In the continental subspecies of Black-tailed Godwit *Limosa limosa limosa*, observations of colour-marked individuals also showed that earlier-arriving birds have longer arrival–laying gaps, such that there is no correlation between the timings of arrival and laying (Lourenço *et al.* 2011). Despite this apparent potential to advance laying, the Dutch population has not shown an advance in laying date since the 1970s, suggesting constraint(s) on the population's capacity to respond to advancing environmental conditions (Schroeder *et al.* 2012). We also found considerable variation and low individual consistency in the arrival–laying gap, mainly related to variation in laying dates. Previous studies have similarly shown lower consistency in laying than arrival dates in Godwits (Lourenço *et al.* 2011, Gill *et al.* 2014).

After arrival, Godwits may have to accumulate resources with which to breed (Klaassen *et al.* 2001) or wait for the arrival of the previous year's mate (Gunnarsson *et al.* 2004). In addition, there is considerable interannual variation in laying date due to spring temperature (Alves *et al.* 2019), probably due to the difficulty of concealing nests when vegetation growth is slow early in the season (Thorvaldsson *et al.* 2005, Laidlaw *et al.* 2020). Thus, a range of social and physical factors could contribute to reduced consistency in the timing of events as the breeding season progresses. Pre-laying visits to the breeding territory may also offer an opportunity to monitor such factors. Indeed, if temporal (and spatial) consistency is linked to mate retention then, as the breeding seasons progresses following re-mating, individual timing may be increasingly determined by environmental factors and thus the consistency of those timings decreases.

We also found no link between migratory or breeding phenology and nest survival, which tended to be constant throughout the season. The daily nest survival of 0.98 in this study is in line with previous estimates of 50–75% hatching success (Gill *et al.* 2007) and previous work also suggested consistently high nest survival throughout the season (Alves *et al.* 2019). Nevertheless, re-nesting occurred after 50% of first nesting attempts in our study, including after attempts estimated to have hatched successfully. This suggests a relatively high rate of chick mortality. We found no seasonal trend in propensity to re-nest, in contrast to studies in other migratory bird systems which

have found more frequent re-nesting with early arrival (Méndez *et al.* 2022) or early nesting (Verhoeven *et al.* 2020, Donelan *et al.* 2021). However, our study had a small sample of eight birds spread over 10 breeding seasons: it is therefore very possible that any within-season trend would be difficult to detect given the strong, temperature-related interannual and geographical variation in nesting phenology (Alves *et al.* 2019).

In this study, we complemented life-long tracking of Icelandic Black-tailed Godwits using colour-rings with snapshot pictures derived from remote tracking technologies, in order to elucidate a crucial period of the annual cycle which has proven difficult to study (see Verhoeven *et al.* 2020). Later-arriving Godwits are able at least partly to catch up with earlier-arriving individuals by shortening the time between arrival and breeding events. Although nest success rates do not vary seasonally, breeding as soon as possible after arrival is still likely to be beneficial because offspring recruitment probabilities decline seasonally (Alves *et al.* 2019, Nightingale 2022).

Using electronic tracking data, we generated estimates of nest locations which appear plausibly close to known locations used by individuals prior to this study, and estimates of nest survival that are consistent with field-based investigations. This method also avoids site-biases of various kinds (Li *et al.* 2023). The use of tracking to derive estimates of breeding locations, timing and multiple breeding attempts may therefore be a valuable outcome of the growing quantities of tracking data available for migratory birds, in particular those that breed in difficult-to-study regions or habitats.

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AUTHOR CONTRIBUTIONS

Josh Nightingale: Writing – original draft; writing – review and editing; conceptualization; formal analysis; methodology; visualization; investigation; software. **Jennifer A. Gill:** Conceptualization; writing – original draft; supervision; writing – review and editing; funding acquisition. **Tómas G. Gunnarsson:** Writing – review and editing; investigation. **Afonso D. Rocha:** Investigation; data curation; writing – review and editing. **Ruth A. Howison:** Investigation; data curation; writing – review and editing; project administration. **Jos C. E. W Hooijmeijer:** Investigation; writing – review and editing; project administration; data curation. **Theunis Piersma:** Writing – review and editing; project administration; funding acquisition; conceptualization. **José A. Alves:** Conceptualization; writing – original draft; writing – review and editing; investigation; data curation; supervision; funding acquisition; project administration; visualization.

ETHICAL NOTE

None.

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CONFLICT OF INTEREST

We have no conflicts of interest to disclose.

Data Availability Statement

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

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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. Locations per day for Sarilhos.

Appendix S2. Comparison of tracking- and field-derived estimates of phenology.

Appendix S3. SEM including only 1 year of tracking per individual.

Appendix S4. Outputs and diagnostics from nest survival model.

Appendix S5. JAGS model code for nest survival model.