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Unconventional life history in a migratory shorebird: desegregating reproduction and migration

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Conventional life-history theory predicts that energy-demanding events such as reproduction and migration must be temporally segregated to avoid resource limitation. Here, we provide, to our knowledge, the first direct evidence of 'itinerant breeding' in a migratory bird, an incredibly rare breeding strategy (less than 0.1% of extant bird species) that involves the temporal overlap of migratory and reproductive periods of the annual cycle. Based on GPS-tracking of over 200 female American woodcock, most female woodcock (greater than 80%) nested more than once (some up to six times) with short re-nest intervals, and females moved northwards on average 800 km between first and second nests, and then smaller distances (*ca* 200+ km) between subsequent nesting attempts. Reliance on ephemeral habitat for breeding, ground-nesting and key aspects of life history that reduce both the costs of reproduction and migration probably explain the prevalence of this rare phenotype in woodcock and why itinerant breeding so rarely occurs in other bird species.

1. Introduction

Life-history theory predicts that resource limitations constrain when energy-demanding events such as reproduction occur and prohibits reproduction from overlapping with other energy-demanding events such as migration [1–3]. For most animals, timing of reproduction coincides with the period of the year when

Table 1. Avian species suspected of being itinerant breeders with the nature of the evidence (direct versus indirect) and associated citations.

common name	latin name	nature of the evidence[a]	citations
common quail	*Coturnix coturnix*	indirect	Moreau [26]
eared dove	*Zenaida auriculata*	indirect	Bucher [27]
Eurasian dotterel	*Charadrius morinellus*	indirect	Whitfield, in Wernham *et al.* [28]
yellow-billed cuckoo	*Coccyzus americanus*	indirect	Rohwer *et al.* [29]
hooded oriole	*Icterus cucullatus*	indirect	Rohwer *et al.* [29]
orchard oriole	*Icterus spurius*	indirect	Rohwer *et al.* [29], Rohwer *et al.* [30]
red-billed quelea	*Quelea quelea*	indirect	Ward [31], Jaeger *et al.* [32]
tri-coloured blackbird	*Agelaius tricolour*	indirect	Hamilton III [33], Wilson *et al.* [34]
phainopepla	*Phainopepla nitens*	indirect	Baldassarre *et al.* [35]
water rail	*Rallus aquaticus*	indirect	Lislevand *et al.* [36]
American woodcock	*Scolopax minor*	direct	Slezak *et al.* [37]

[a]'Direct evidence' includes data on individuals that have resided in two distinct regions during the breeding season and were confirmed nesting in each region; 'indirect evidence' includes data on individuals that inhabit different regions during the breeding season but not confirmed breeding in both.

food resources are most available [4–6]. For species inhabiting seasonal environments, the timing of reproduction may have an outsized effect on breeding success and annual productivity [7–9], in part because food resources typically reach a seasonal peak in abundance and then decline over time [10–14]. Many migratory species time their northward migrations to coincide with food resources at important stopover locations to replenish fat reserves for migration and breeding [15]. Herbivores provide classic examples of such seasonal movements [16–18] including long-distance migratory geese that 'ride the green wave' north each spring as they prepare over time for breeding in the Arctic [19–21]. Across the diversity of life histories apparent in animals today, the vast majority of seasonal movements in migratory species conform to predictions of life-history theory in the sense that migration and reproduction occur during discrete periods and seldom overlap during the annual cycle in large part because of the substantial energy demands associated with breeding [3,22,23].

For migratory birds, balancing the timing of reproduction with that of migration has direct consequences: if individuals migrate too early in spring, their arrival may not coincide with peak resource abundance when raising young [6,24,25]; if they arrive too late, they may not have enough time to successfully raise young to independence prior to southward migration [25]. Only a few migratory bird species (less than 0.1% of extant species; table 1) have apparently defied conventional circannual patterns and overlap migratory and reproductive periods [23]. For these bird species, individuals breed then migrate and breed again, a breeding system known as 'itinerant breeding' or 'migratory double breeding' [29,35]. Careful consideration of such rare phenotypes may pose challenges to common assumptions about constraints on organic form and function [38] and allow us to identify ecological and physiological limitations that have produced them [39]. Although suspected in several species (table 1), evidence for this rare phenotype based on movement patterns of individuals has only been partly confirmed to date in three migratory bird species: redbilled quelea ([32] *Quelea quelea*), tri-coloured blackbird ([34] *Agelaius tricolour*) and phainopepla ([35] *Phainopepla nitens*). Direct evidence for itinerant breeding requires tracking individual movements during the breeding season while confirming breeding in multiple regions; such evidence is not available to date for any of these purported itinerant breeders. Herein, we provide, to our knowledge, the first direct evidence of itinerant breeding from detailed GPS tracking of greater than 200 individually marked female American woodcock (*Scolopax minor*), a migratory shorebird that inhabits forests in eastern and central North America.

We closely monitored the movement patterns of GPS-tagged female woodcock across their entire range over two years (2021–2022) to document migration movements as well as nest initiation and incubation. For 26 females that exhibited short (e.g. <20 m) step-lengths in sequence over several days (electronic supplementary material, figure S1), we field-verified that these distinct movement patterns were associated with an actively nesting individual. We then used the nestR package [40] to retroactively locate nest attempt(s) for a larger sample of females ($n = 272$) that were captured and tagged over 4 years (2019–2022); we were also able to confirm correct classification of 92% (24 of 26) of our field-verified nesting attempts when we used this approach (see Methods). A subset of females ($n = 55$) were tracked frequently (GPS locations every 1–3 days; $\bar{x} = 4.3$ locations every 4 days) over an extended portion of the breeding season (20 February to 1 June). For these individuals we were able to evaluate the overlap between migration and reproduction, estimate key components of their reproductive strategy (i.e. number of nest attempts, attempt duration and re-nest time), and determine how this strategy differed for young versus older woodcock (*ca* 1 yr old versus ≥2 yr old females). If woodcock are itinerant breeders, then we predicted that females would regularly and rapidly re-nest after nest failure, that females would migrate north between nesting attempts, and in general there would be considerable temporal overlap between the reproduction and migration periods of the annual cycle.

2. Methods

(a) Satellite transmitter attachment

Thirty-six state, federal and non-governmental organizations helped tag female woodcock throughout eastern North America from Florida, USA northwards to Atlantic Canada (electronic supplementary material, table S1) as part of the Eastern Woodcock Migration

Research Cooperative [41]. Woodcock were captured and leg-banded at night using the night lighting technique [42] or mist-netted during crepuscular periods [43]. We determined age and sex of woodcock in the field using wing feather characteristics [44]. From 1 September 2019 to 1 June 2022, collaborators captured 366 females that were then tagged with 4 g, 5 g or 6 g GPS satellite transmitters (PinPoint Argos 100; PinPoint Argos 125; PinPoint Argos 150; Lotek Wireless, Newmarket, Ontario, Canada) that collected 75 to 150 GPS locations before tag failure. We closely followed protocols outlined in the *Guidelines to the use of Wild Birds in Research* to minimize stress and disturbance of captured birds and we ensured that total mass of marking materials (transmitter, harness and band) did not exceed 4% body mass [45]. The 272 tags still collecting data on or after 1 January annually (electronic supplementary material, table S1) were programmed to transmit GPS locations (±20 m) approximately every 1–3 days, although the actual number of locations recorded was on average 4.3 locations (s.d. = 5.42) every 5 days for the period of time tags were active. The collected locations from all PinPoint tags were uploaded to our Movebank repository.

(b) Field verification: sequential movement distances indicate nesting females

During 2021–2022, we scrutinized the daily GPS locations of females during the window of time encompassing the bulk of courtship activity from 20 February to 1 June each year. Specifically, we measured the step-lengths between subsequent GPS locations for each female in the dataset at least twice a week using the ‘as.traj’ function in the adehabitatLT package [46] in R version 4.2.2 [47]. We recognize that some southerly nesting woodcock may initiate nests earlier than mid-February; however, many tags were still being deployed in the southerly areas during early-February and thus did not start transmitting until mid- to late- February (electronic supplementary material, table S1). When step-lengths were small (less than 20 m) for two to three or more GPS transmissions (electronic supplementary material, figure S1), we notified the nearest collaborator and requested they travel to the point cluster and investigate the site for a nesting female or signs of a successful or failed nesting attempt (e.g. longitudinally split eggshells or crushed eggshells). In total, we field-verified 26 nests (2021: $n = 16$; 2022: $n = 10$) from 22 (2021: $n = 13$; 2022: $n = 9$) individual females including four females confirmed nesting more than once. The step lengths for field-verified nesting females in 2021 (12.6 m, 95% confidence interval (CI): 11.9–13.3 m) were not statistically different ($F_{1,178} = 0.43$, $p = 0.52$) from 2022 (14.2 m, 95% CI: 12.8–15.6 m) and confirmed that these short step-lengths between consecutive *ca* daily locations indicated an incubating female woodcock. In addition, there were 11 instances that met these step-length criteria for incubating females but cooperators were unable to find the nest. Such potential false-positive detections probably occurred because female woodcock and their nests are highly cryptic and so easily missed or because nest depredation rates can be high for ground-nesting woodcock ([48] reports 67% failure) and so nests may have gone before cooperators were asked to find the nest. Three of the four females that were found re-nesting migrated a substantial distance northwards from their initial nest attempt (range: 199 to 889 km).

(c) Application to larger (2019–2022) GPS tracking dataset

Given that our tracking data covered the majority of breeding and wintering range of woodcock in North America, we used a more inclusive (1 January to 1 September) as well as restrictive (20 February to 1 June) time period to investigate nesting behaviour of females. Our more inclusive dataset allowed us to include more females that were tracked for variable durations of time and so evaluate population-level patterns of nesting in relation to timing and latitude. By contrast, our more restrictive dataset included only females that were tracked almost daily (on average 3.5 locations every 4 days) from 20 February to 1 June, which includes the approximate range of core breeding activity in the most southerly and northern reaches of the woodcock’s range [43,49–51]. These females tracked throughout the core breeding period allowed us to answer fundamental questions about woodcock breeding ecology such as the total number of nesting attempts, how long nest attempts last on average, how quickly females re-nest, if distance moved between attempts was related to female age, and whether migration distance influenced total number of nest attempts. This dataset also allowed us to relate a female’s nesting sequence to metrics such as distance moved, latitude and week of nesting season.

(d) Population-level patterns of nesting throughout the breeding season (1 January to 1 September)

We used the find_nests() function in the nestR package [40] to identify nesting attempts from our inclusive and restrictive datasets, and used our sample of field-verified nests to assess its accuracy. The find_nests() function identifies potential nests based on revisitations and the amount of time spent within a user specified buffer surrounding each GPS location [40]. Our inclusive dataset included a broader range of start (1 January) and end (1 September) dates for the four nesting seasons (2019–2022) to ensure early- or late-nesting attempts by females were detected [52–54]. Because the step lengths of our field-verified nesting females were on average <20 m in each year, we chose a maximum buffer size of 20 m that females had to stay within for at least 5 days to be considered a nesting attempt. We chose a 5-day window because the satellite tags used in this project require about 5 days to collect three successful GPS locations and transmit to the ARGOS satellite, thus this was typically the minimum number of days over which nesting females could be detected. Woodcock take infrequent incubation recesses [55] and our transmitter schedule was coarse enough that capturing a female off of the nest was unlikely, thus we set the ‘min_d_fix’ parameter to two GPS points, which required two consecutive GPS fixes to fall outside of a 20 m buffer before a nest was considered no longer active. This allowed us to approximate nest attempt start and end dates for each of the female’s nesting attempts. When using the ‘find_nests’ function, we set the ‘discard_overlapping’ parameter to ‘TRUE’ to ensure that only one location would be chosen from a set of temporally overlapping nest attempts. For females that nested more than once, we measured the distance travelled to subsequent nesting attempts using the ‘as.traj’ function in the adehabitatLT package [46] in R.

Our use of short-distance step lengths to identify incubating females could unintentionally include stationary females that had died, and so the following two-step process was used to exclude ‘nests’ from females after they were classified as deceased. We first used the momentuHMM package in R [56] to train a hidden Markov model on a set of known movement states (dead female, alive female but stationary and migratory females) and used this trained model to autonomously classify mortality events in our female tracking dataset. Once the model had identified which females had probably died, we used a R Shiny application to ensure that any individual marked as deceased had (i) 15 locations in a deceased state, and (ii) at least half of deceased locations fell within a threshold distance of the centroid. The threshold distance varied based on landcover owing to differences in GPS accuracy between cover types (range of threshold distances: 3.93–10.85 m). This two-step process identified and excluded 13 females that would have been classified as ‘nesting’ but instead had died during the four breeding seasons.

(e) Individual-level patterns of nesting during the core breeding period (20 February to 1 June)

Of the 272 females tracked from 1 January to 1 September, a subset ($n = 55$ females) with greater than 10 GPS locations were tracked throughout the entire period of core breeding activity observed in the southern and northern reaches of the woodcock's breeding range (20 February to 1 June; [52–54,57]) during at least one of the 4 years of the study. We used this subset of 55 females to evaluate the total number of nesting attempts by each female in a given season, the date and estimated duration of each nesting attempt, and how quickly females re-nested. Like the inclusive dataset, we measured the distance moved for females that nested more than once using the 'as.traj' function in the adehabitatLT package [46] in R, and then related distance moved between attempts to female age. This dataset also allowed us to relate a female's nesting sequence to metrices such as distance moved, latitude and week of nesting season because females had complete tracking data (i.e. the entirety of the core breeding period) unlike the females in the more inclusive dataset that were often tracked for a more brief and variable period of time.

(f) Statistical methods

(i) Population-level patterns of nesting throughout the breeding season (1 January to 1 September)

We calculated nest attempt duration for all nests by subtracting the estimated nest attempt end date by the nest attempt start date using the 'difftime' function in R. Nests that lasted 19 or more days were considered likely to be successful (mean incubation period is 21 days for precocial woodcock; [58], range is 19 to 22 days; [49]). To determine if week of nesting season, latitude, or the additive effect of these two variables best predicted nest success, we used logistic regression models implemented using a generalized linear model and logit-link function in the stats package in R. However, we did not include the additive model in our final model comparison because latitude was not a significant predictor. We performed model selection using Akaike information criterion adjusted for small sample sizes ($\mathrm{AIC_c}$) using the 'aictab' function in the AICcmodavg package [59]. We considered models with $\Delta\mathrm{AIC_c}$ values ≤ 2 to have equivalent evidence of being the top model(s) [60]. Finally, we used the 'geom_smooth' function in the ggplot2 package in R to plot a smoothed trend line (loess line) so that we could visualize the relationship of ordinal date and latitude with the distance moved between nesting attempts for our entire dataset of tagged females.

(ii) Individual-level patterns of nesting during the core breeding period (20 February to 1 June)

For each of the 55 females tracked throughout the core breeding period, we also calculated nest attempt duration for every documented nest by subtracting nest attempt end date by nest attempt start date using the 'difftime' function in R. We also used the 'difftime' function to calculate re-nest time for females that nested more than once by subtracting the attempt start date by the attempt end date of the prior nesting attempt. We conducted an analysis of variance (ANOVA) using the 'aov' function in R to determine whether nest attempt duration and re-nest time differed among the first, second, third or fourth nest attempt. We had too few fifth ($n = 6$) and sixth ($n = 1$) nesting attempts to include them for this statistical analysis. We also used an ANOVA to determine if distance travelled to subsequent nest attempt varied by female age (second year (SY) versus after second year (ASY)) or nest attempt sequence (1–4).

3. Results

(a) Population-level patterns: nesting occurs from January–August, and females move north between nesting attempts

We identified 336 woodcock nesting attempts from 153 of 272 (56.25%) females that transmitted locations between 1 January and 1 September during the 4 years (i.e. 2019 to 2022). The 119 females that were not detected nesting were typically tracked for short periods of time on average (43.39, 95% CI: 37.34–49.43 days) and half of these 119 females' tags had 35 or less transmissions, a period too short to reliably detect if these females attempted nesting. Like Whiting [54], we found that a majority of nests were initiated no earlier than mid-February; only 72 (22%) of 336 were initiated prior to 20 February, all in more southerly areas of the woodcock's range ([61] reports Alabama, Arkansas, Florida, Georgia, Louisiana, Maryland, North Carolina, New Jersey, Oklahoma, South Carolina and Virginia). Females that nested earlier in the spring tended to move further to subsequent nesting attempts than those later in the season (figure 1*a*). In addition, females tended to move a shorter distance (km) between subsequent nesting attempts as latitude increased (figure 1*b*). We found that about half (57%) of all nesting attempts were long enough in duration to have hatched chicks (≥19 days incubation) although such an estimate of nest survival is inflated because our methodology limited our ability to detect short-lived nests (i.e. lasting ≤3 days or before the tag collected three GPS transmissions). An incubation period of 19 or more days also does not necessarily equate to successfully fledged chicks because brood loss is not considered. Our top model ($\Delta\mathrm{AIC_c} \leq 2$) with week of nesting season predicting nest success held 86% of the cumulative weight of our three model sets (electronic supplementary material, table S2). This model suggests that the probability of a successful nesting attempt increased (week coefficient = 0.05, 95% CI: 0.018–0.083**)** as the nesting season progressed.

(b) Individual-level patterns: females first nest on 'wintering areas' and often renest many times (up to 6) as they migrate north

We identified 144 likely nesting attempts from 52 of the 55 females (95%) that were tracked every 1 to 3 days throughout the core breeding season (20 February to 1 June in a given year), and 42 of these 52 females (81%) had more than one nesting attempt (figure 2*a*). We found no statistical difference ($F_{3,133} = 1.86$, $p = 0.14$) in nest duration between nesting attempts 1 to 4 (figure 2*b*), so we report the population mean (16.47, 95% CI: 15.65–183 days). We also found no statistical difference ($F_{2,82} = 2.46$, $p = 0.092$) in re-nest time between nesting attempts 1 to 4 (figure 2*c*) so we report the population mean (23.95, 95% CI: 20.04–27.86 days; range: 1–70 days). However, distance moved between nesting attempts 1 to 4 (figure 2*d*) significantly differed

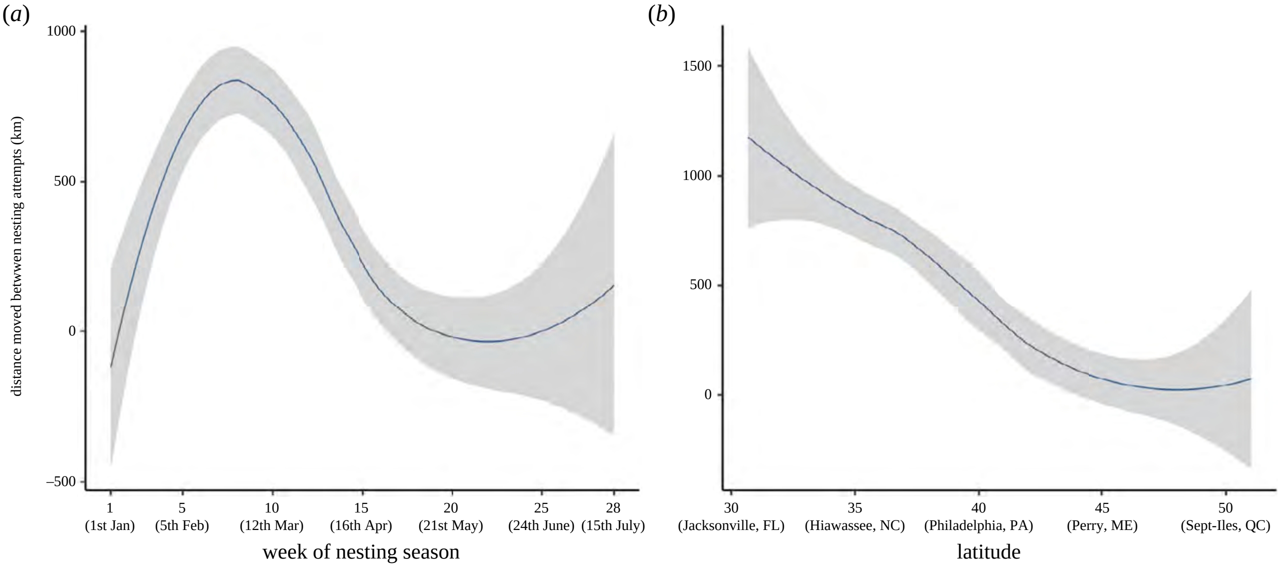

Figure 1. Movement patterns between nesting attempts for a population of individually marked females. (*a*) Smoothed loess line with 95% confidence bands depicting the moving average of distance moved between nesting attempts by week of nesting season for 337 nesting attempts from 154 females tracked annually from 2019 to 2022. (*b*) Smoothed loess line with 95% confidence bands depicting the moving average of distance moved between nesting attempts by latitude for 337 nesting attempts from 154 females tracked annually from 2019 to 2022.

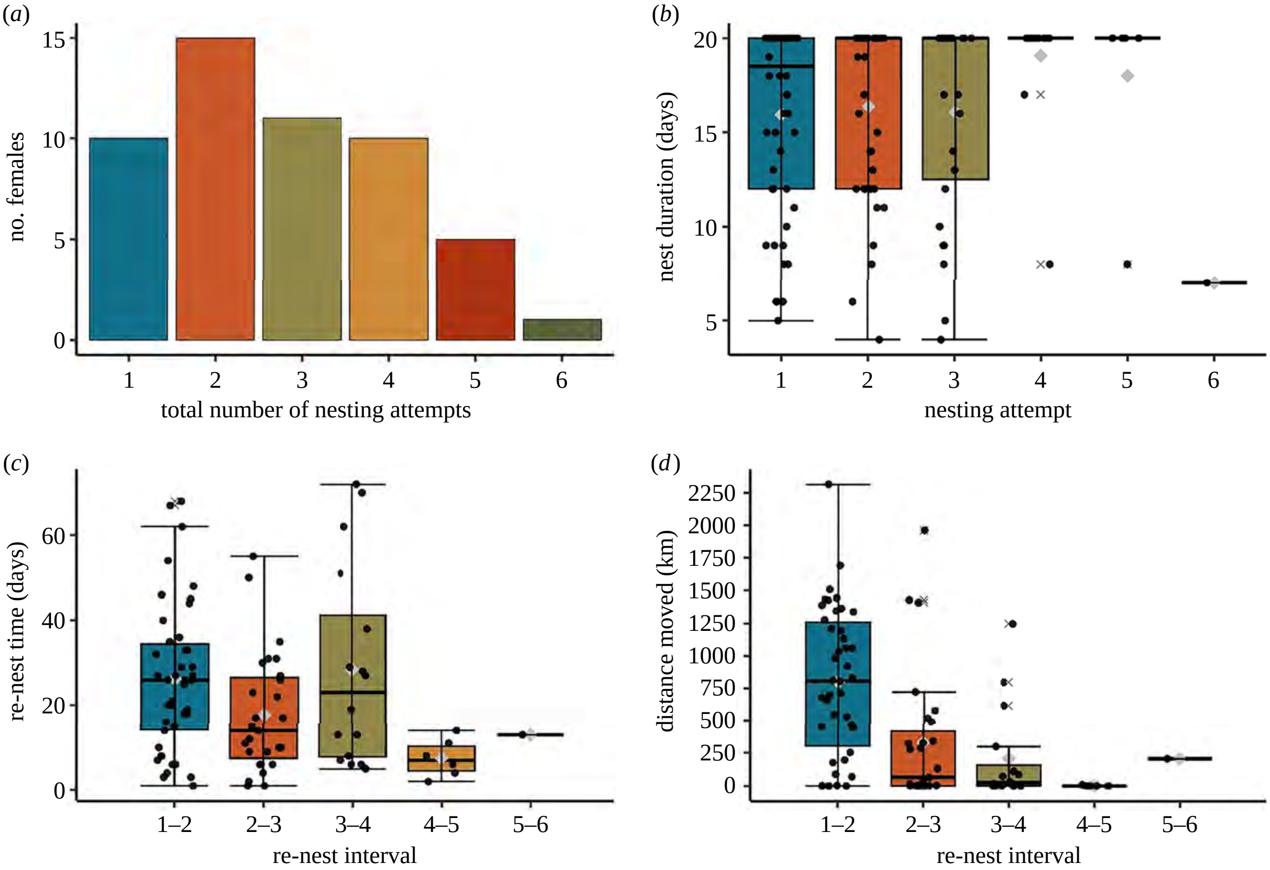

Figure 2. Nesting characteristics for individually marked females. (*a*) Total number of females with one or more nest attempts, (*b*) nest attempt duration, (*c*) re-nesting interval time between each nest attempt, and (*d*) distance moved between nesting attempts for 144 nesting attempts for 52 of 55 female American woodcock that nested and were tracked almost daily from 20 February to 1 June in a given year (2019–2022). Boxes indicate median, mean (diamond in grey), 25% and 75% quartiles. Points represent raw data values, and whiskers represent the greatest and least values within 1.5 times the interquartile range over the 75th percentile. Outliers are presented as a cross-hatch (X).

($F_{2,81} = 10.42$, $p < 0.05$). Females moved further between nesting attempt 1 to 2 than their subsequent nesting attempts regardless of location or latitude although the mean distance travelled after attempts 2 and 3 did not statistically differ (mean of attempt 1 to 2 (799.05 km, 95% CI: 620.81–977.29 km); mean of attempt 2–3 (330.62 km, 95% CI: 128.37–532.88.17 km); mean of attempt 3–4

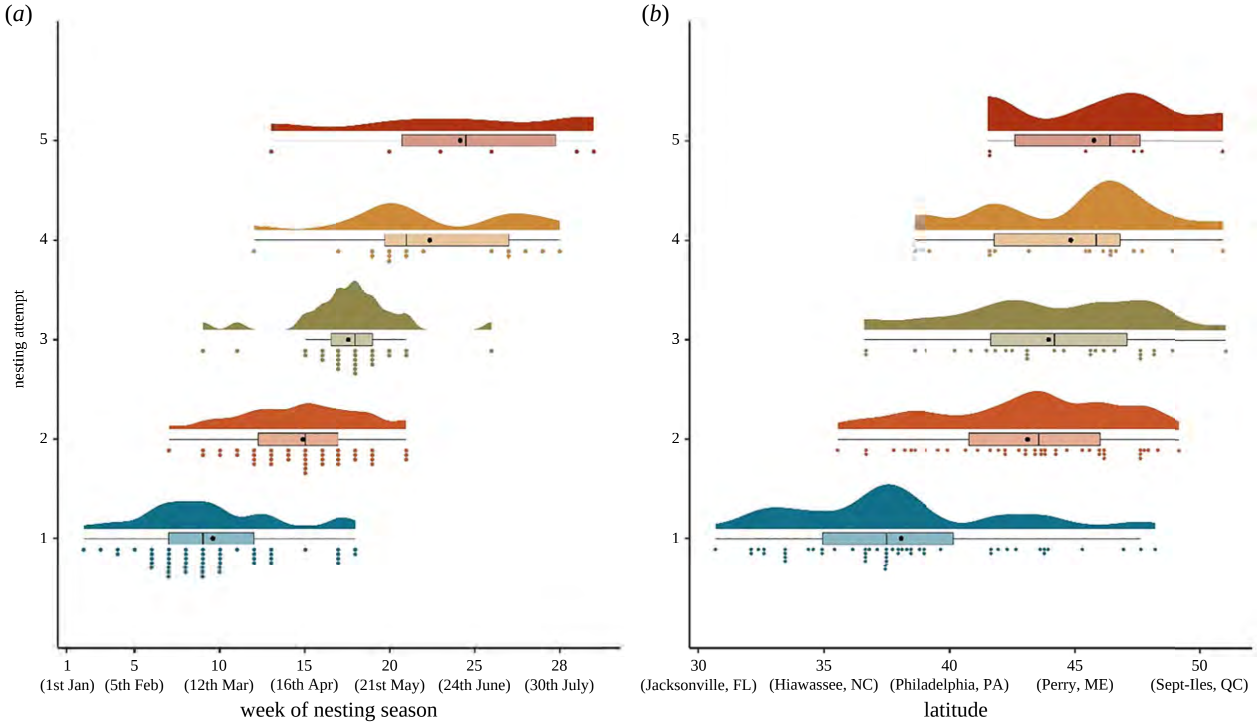

Figure 3. Nest sequence by week and latitude for individually marked females. (*a*) Raincloud plot showing the distribution of nest initiation dates by week and (*b*) by latitude for each subsequent nesting attempt (up to five attempts) for the 144 nesting attempts for 52 of 55 female American woodcock that nested and were tracked almost daily from 20 February to 1 June in a given year (2019–2022). Boxes indicate median, mean (black point within box plot), 25% and 75% quartiles. Points represent raw data values, and whiskers represent the highest and lowest values within 1.5 times the interquartile range over the 75th percentile.

(205.74, 95% CI: 10.89–400.60 km)). Distance moved between subsequent nesting attempts did not statistically differ for SY versus ASY females ($F_{1,77} = 3.31$, $p = 0.07$) although older ($n = 44_{\mathrm{ASY}}$) females moved further on average (619.20 km, 95% CI: 432.48–805.91 km) between attempts than younger ($n = 71_{\mathrm{SY}}$) females (388.84 km, 95% CI: 270.42–507.25 km). Most first nests occurred before 12 March (figure 3*a*) and were below 40° N latitude (range: 30° N to 48° N latitude; figure 3*b*) within areas outside of the area traditionally reported as the woodcock breeding range [58]. We found that woodcock had a prolonged nesting season, with some nests initiated as early as 9 January and as late as 10 August, and that females nesting at higher latitudes were typically those that had already nested at lower latitudes (figure 3*b*). Between 1 January and the final tag transmission, each female migrated northwards on average 1348.28 km (95% CI: 1210.68–1485.87 km); however, the total distance a female migrated did not relate to its total number of nesting attempts ($F_{1,53} = 0.86$, $p = 0.36$). Many females first nested in the southern portion of the woodcock's range (mean 38.03° latitude, 95% CI: 36.85–39.21° latitude), and then continued northwards to nest again in a direction typical of migratory woodcock (electronic supplementary material, figure S2).

4. Discussion

As we have shown for American woodcock, itinerant breeders can rapidly switch between reproductive and migratory states and this challenges the fundamental assumption that endocrine mismatch forces divergent partitioning of certain life-history traits (i.e. reproduction and migration) across the annual cycle [30,35]. Flexible timing in the annual cycle of birds is thought to arise when the breeding season is prolonged (e.g. non-migrants that are not constrained by periods of migration) and when there is great annual variation in environmental cues (e.g. climatic conditions and shifting food availability) which makes consistent timing of reproduction less beneficial [35,62]. However, we do not think this set of factors alone adequately explains the unusual breeding strategy of woodcock and potentially the other purported itinerant breeders that have unconstrained themselves from distinct breeding sites and seem to migrate between breeding attempts (table 1).

Itinerant breeding birds documented to date share the following traits: a relatively low cost of reproduction and reliance on ephemeral habitats (e.g. early successional forest for American woodcock [23,35]). These traits are important in explaining itinerant breeding in woodcock, but other well understood aspects of the woodcock's life history seem potentially relevant in explaining how this could evolve in woodcock and potentially other itinerant breeders (figure 4). Like many shorebirds, woodcock consistently lay four eggs and produce precocial young at hatch [63]. Costs of reproduction and migration for female woodcock are estimated to be relatively small compared to other Arctic breeding shorebirds, and like other shorebirds females typically rely on exogenous nutrients acquired upon arrival to breeding sites for egg production [64,65]. However, woodcock are relatively unusual shorebirds in that females also store appreciable fat in preparation for reproduction [64,66]. The considerably shorter distance migrations than that of most other shorebirds along with their reliance on exogenous nutrients may explain why females can re-nest frequently even while providing uniparental care [67]. Woodcock are among the earliest breeding

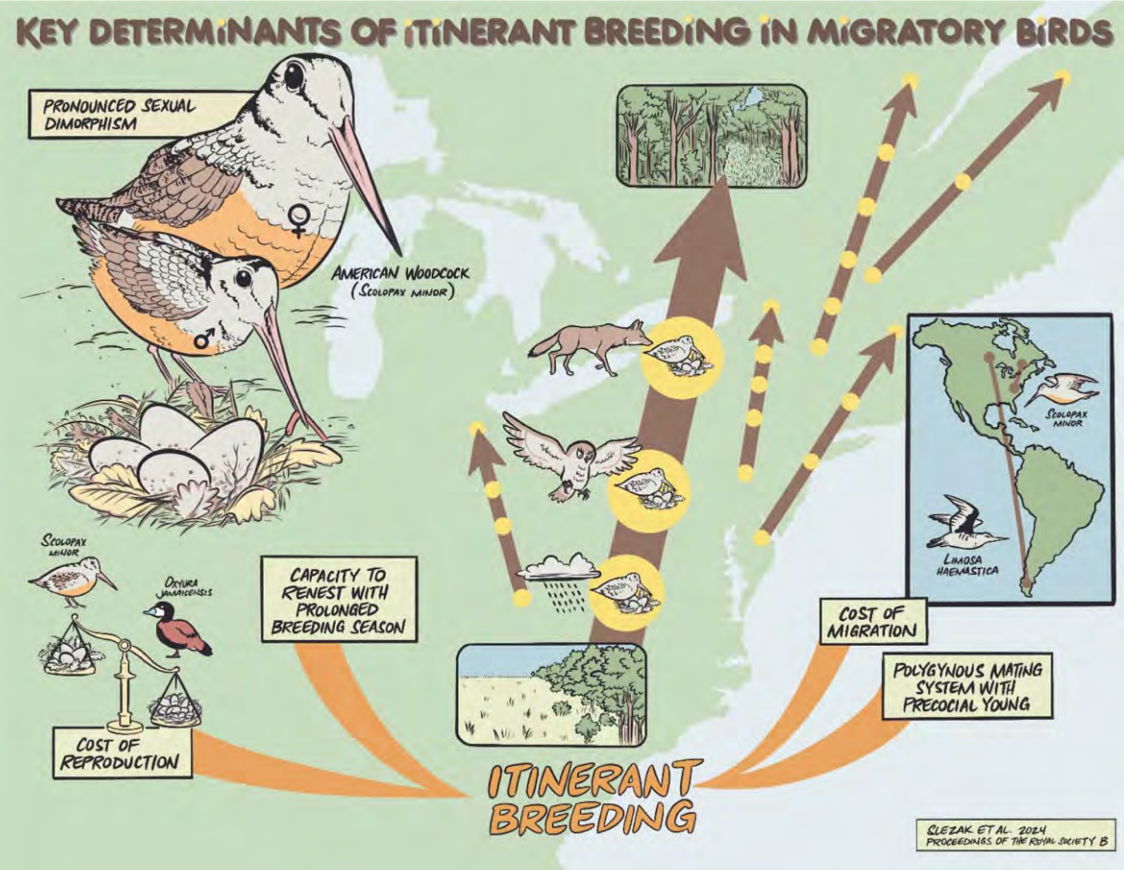

Figure 4. Life-history traits and ecological conditions related to the occurrence of a rare breeding strategy, itinerant breeding, in migratory birds. Itinerant breeding involves desegregating in time the reproduction and migration periods such that nesting occurs multiple times while migrating between nest attempts. Selection for itinerant breeding among migratory birds requires reduced costs of migration and reproduction along with a mating system that permits mate finding along migratory routes and the ability to re-nest. For woodcock, females alone build the ground-nest, lay the initial four-egg clutch, incubate and tend the precocial young. Reversed sexual size dimorphism is pronounced in woodcock and thus for the large-bodied females the costs of producing a clutch is relatively low. Like many ground-nesting birds, nest predation is common, and thus the ability to quickly re-nest and prolong the breeding season is a key determinant of lifetime reproductive success. What makes itinerant breeders quite unusual is that instead of choosing to re-nest nearby, they migrate between nesting attempts. Woodcock initiate breeding very early each year (January/February) often at or near wintering areas with males courting and seeking mating opportunities throughout their migration to northern breeding areas. Their polygynous mating system along with the relatively low costs of reproduction allow female woodcock to find mates and re-nest several times (up to six) as they track spring resource pulses northwards during spring migration.

birds in the Northern Hemisphere and commence nesting when environmental conditions are often not favourable for other species [68,69]. As a consequence, woodcock are more susceptible to unpredictable environmental conditions that could lead to nest failure (i.e. late frosts, spring snow/ice storms and summer heat waves) than species with shorter reproductive windows. This phenological pattern is similar to the phainopepla system where frost or drought can kill the mistletoe crop and disrupt early breeding [35]. An extended reproductive period, with the opportunity for multiple renesting attempts may allow woodcock to better cope with nest failure associated with stochastic weather events as well as predation. The unusually large size of female woodcock relative to males [70] and a total fresh egg mass that is a relatively small percentage of the female's mass [71], combined with a simple nest (scrape lined with leaf litter) and precocial young [58] reduces the relative cost of each nesting attempt and may facilitate the rapid (figure 2*c*), frequent (figure 2*a*), and geographically expansive re-nesting behaviour (figure 2*d*) of this itinerant breeder. The reduced costs of each nesting attempt combined with their reliance on exogenous nutrients for egg laying may also select for woodcock to track seasonally abundant food and nesting cover as they 'follow the spring thaw north' (figure 5) much like avian herbivores that 'ride the green wave' as they accumulate fat stores on their way to high-latitude breeding areas [16,17].

The recognition that woodcock have evolved an itinerant breeding strategy also helps explain some of the long-recognized, unusual aspects of the life history of this species: (i) extended breeding seasons (i.e. nesting January to August [52,54,72,73]) with males initiating courtship displays as early as January in the south [51,74], (ii) re-nesting as a rule rather than an exception [67] and its frequency declining in years with late spring green-up [75], (iii) females that exhibited peculiar movement patterns (e.g. brooding females banded in the south later harvested in the far north of their range [76]), and (iv) extreme levels of reverse sexual size dimorphism compared to other shorebirds [70]. The breeding system of woodcock has been characterized as polygynous with males defending territories in which they perform courtship displays and females nesting near or in these territories, but with no formation of a social pair bond, and no evidence of multiple paternity within broods [58]. Unlike prior studies, we directly tracked individual females to reveal multiple nesting attempts interrupted by long-distance movements along their northly migratory paths in spring (figure 5). This has allowed us to confirm itinerant breeding at the individual (figure 2) and population level

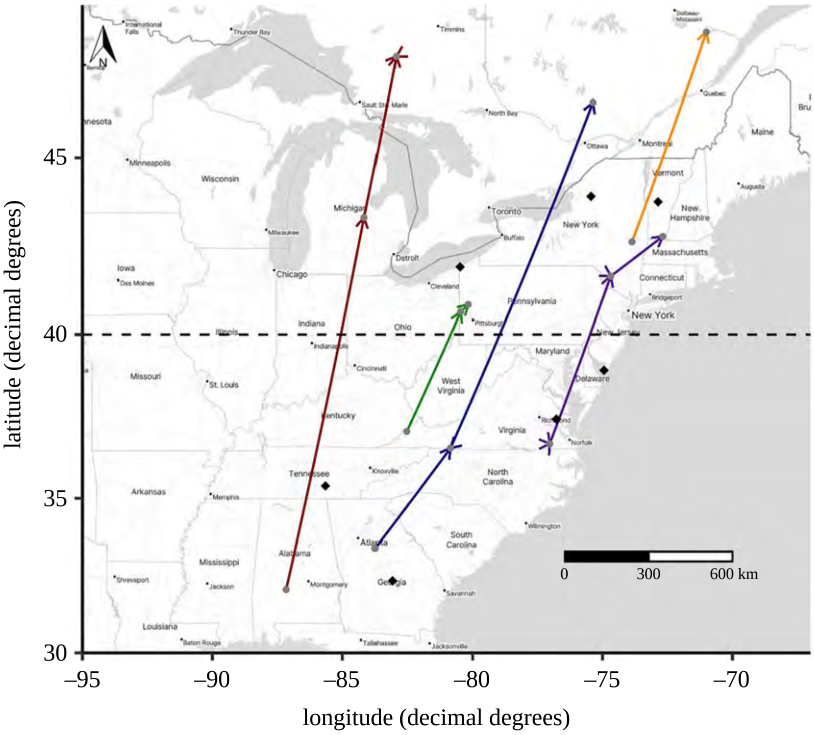

Figure 5. Example movement patterns for individually marked nesting females during spring migration. The location of nests for the few females that nested only once ($n = 10$) are displayed as black diamonds. Lines connecting nesting locations (circles) provide an example GPS track for a female that re-nested twice (yellow), three times (green), four times (blue), five times (red) and six times (purple). Arrows show the northerly direction of female movement between each nest attempt. Arrowheads without a visible line segment were re-nests that were short distances from the previous nest attempt (typically ≤5 km), and the direction of the arrowhead indicates the direction moved from the previous nesting attempt. The black dashed line at 40° N latitude represents the southern extent of the area considered the core region of woodcock breeding activity. GPS tracks of all females that nested ($n = 52$) are provided in the electronic supplementary material, figure S2.

(figure 1). Prior studies of itinerant breeders (table 1) have been unable to identify the locations of multiple breeding attempts and have instead relied on the movement patterns of a few individuals which had presumably nested before migrating to a new breeding site [35]. The large proportion of woodcock that re-nested (figure 2*a*; 81% of all nesting females) and their impressive migratory movements (up to 2315 km) between breeding attempts (electronic supplementary material, figure S2), combined with the movement patterns and nesting attempts observed in the entire population (figure 1), suggest that itinerant breeding is prolific among woodcock. For woodcock, we hypothesize that certain aspects of their life history (i.e. reverse sexual size dimorphism, clutch size limitations, precocial young, mixed capital-income breeding strategy [6] have reduced overall reproductive cost, allowing them to nest in early-successional forests over extended periods of time and track thawing soils and seasonally abundant nesting cover during spring. It remains to be determined if these ecological and life-history factors also explain itinerant breeding in other species and how migratory species at large adapt to changing environments.

Ethics. All woodcock trapping, handling and tagging activities were conducted in accordance with the University of Rhode Island Animal Care and Use Guidelines under Animal Care and Use Protocol AN10Ã¢02Ã¢017 and the University of Maine Institutional Animal Care and Use Committee (protocols A2017_05_02 and A2020_07_01).

Data accessibility. All female capture information, GPS tracking data downloaded from Movebank and R code is available online in our Zenodo repository [37]. Supplementary material is available online [77].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. C.R.S.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; E.J.B.: conceptualization, data curation, funding acquisition, investigation, methodology, resources, supervision, writing—review and editing; A.M.R.: funding acquisition, writing—review and editing; L.A.B.: investigation, visualization, writing—review and editing; R.D.: investigation, visualization, writing—review and editing; A.C.F.: conceptualization, investigation, writing—review and editing; S.J.C.: writing—review and editing; G.B.: investigation; B.C.: investigation; G.C.: investigation; J.D.: investigation; C.L.G.: investigation; W.H.: investigation; M.H.: investigation; D.L.H.: investigation; S.M.: investigation; S.W.M.: investigation; T.C.N.: investigation; J.B.P.: investigation; C.R.: investigation, writing—review and editing; J.C.S.: investigation; J.N.S.: investigation, writing—review and editing; R.T.: writing—review and editing; L.W.: investigation; J.E.K.: investigation; M.T.: investigation, writing—review and editing; S.R.M.: conceptualization, funding acquisition, investigation, methodology, supervision, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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