Bird Study

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tbis20

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To cite this article: Jenny L. Donelan, Catriona A. Morrison, Iain R. Barr & Jennifer A. Gill (2021): Consequences of spring arrival dates for the breeding phenology of migratory warblers, Bird Study, DOI: 10.1080/00063657.2021.1962804

To link to this article: https://doi.org/10.1080/00063657.2021.1962804

BIRD STUDY
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Consequences of spring arrival dates for the breeding phenology of migratory warblers

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ABSTRACT

Capsule: Early male arrival on the breeding grounds results in early pairing but not early nesting in Chiffchaffs *Phylloscopus collybita*, and Chiffchaffs can nest, fail, and re-nest before Willow Warblers *Phylloscopus trochilus* begin nesting.

Aims: To quantify the consequences of timing of arrival for the subsequent timing of pairing, nesting, and re-nesting of short-distance (Chiffchaff) and long-distance (Willow Warbler) migrants.

Methods: The arrival dates of 118 Chiffchaffs and 20 Willow Warblers were measured from March to June over 10 weeks in Foxley Wood nature reserve, Norfolk. Colour-ringing of 56 Chiffchaffs (55 males, 1 female) and 11 Willow Warblers (10 males, 1 female) was used to relate individual arrival dates to timing of male pairing, clutch initiation, and re-nesting.

Results: Male Chiffchaffs started to arrive in early March and increased rapidly in number until early April, while the arrival of male Willow Warblers began in early April. Early-arriving male Chiffchaffs paired earlier than later-arriving individuals, but timing of clutch initiation was unrelated to male arrival dates. Early nesting by Chiffchaffs allowed replacement clutches following nest loss, the earliest of which occurred 12 days after the first Willow Warbler male had paired.

Conclusions: Although early arrival in male Chiffchaffs does not translate into earlier nesting, timing of nesting in Chiffchaffs was sufficiently early to allow time for replacement clutches following nest loss. The later arrival of Willow Warblers is likely to mean fewer opportunities for replacement clutches following nest loss. This difference in breeding phenology could therefore contribute to differences in productivity between the species, especially if nest failure rates are high.

ARTICLE HISTORY
Received 5 February 2019
Accepted 18 December 2020

In migratory birds, the timing of spring arrival on their breeding grounds can vary greatly, with longer distance migrants tending to arrive later than species that undertake shorter migratory journeys (Gunnarsson & Tómasson 2011, Jonzén *et al.* 2006). This variation in the timing of arrival can lead to intra- and inter-species variation in the timing of breeding (Mason 1995, Smith & Moore 2005, Tryjanowski *et al.* 2004). Early arrival of short-distance migrants on the breeding grounds could potentially facilitate earlier breeding (Meltofte *et al.* 2018, Woodworth *et al.* 2016), which may be beneficial if it allows time for multiple nesting attempts or the laying of replacement clutches if early nesting attempts are unsuccessful. Rates of nest loss (e.g. through predation of eggs) and subsequent re-nesting can be high, particularly in ground-nesting species (Newton 1998), and replacement clutches may, therefore, make an important contribution to overall productivity in these species (Morrison *et al.* 2015a, Thompson *et al.* 2001). However, relatively little is known about the consequences of arrival phenology on the phenology of subsequent nesting and re-nesting events.

To explore the links between timing of spring arrival, pairing, clutch initiation, and re-nesting following nest loss, within- and between-species, we tracked individual Common Chiffchaffs *Phylloscopus collybita* (hereafter Chiffchaff) and Willow Warblers *Phylloscopus trochilus* during the breeding season. Chiffchaff is a short-distance migrant that overwinters in areas stretching from North Africa to Europe, and begins to arrive on its UK breeding grounds during March (Balmer *et al.* 2013). In contrast, Willow Warbler is a long-distance migrant

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that overwinters in sub-Saharan Africa, and primarily arrives at its UK breeding grounds during April (Balmer *et al.* 2013). Willow Warbler populations have declined sharply in abundance in the south and east of the UK in recent decades, while Chiffchaff populations have increased over the same period (Morrison *et al.* 2010, Morrison *et al.* 2013). Recent work has linked the decline in Willow Warbler populations in these regions to low levels of productivity (Morrison *et al.* 2015a, 2016a), while Chiffchaff populations show little latitudinal variation in productivity (Eglington *et al.* 2015). If nest loss rates are high, then these differences in productivity could potentially be influenced by the earlier arrival of Chiffchaffs enhancing their capacity to lay replacement clutches. The aims of this study were, therefore, to quantify: (1) arrival dates of male and female Chiffchaffs and Willow Warblers, (2) associations between individual male arrival and subsequent pairing and clutch initiation dates, and (3) the frequency and timing of replacement clutches (re-nesting attempts following nest loss).

Methods

Measuring individual arrival dates

This study took place in Foxley Wood nature reserve, Norfolk (52.7620° N 1.0413° E), owned by Norfolk Wildlife Trust. The site consists of 123 ha of predominantly deciduous tree species interspersed with conifers and dense understory vegetation, with an abundance of suitable nesting habitat for both Chiffchaff and Willow Warbler. Standard territory mapping methods (Bibby 2000) were used to establish Chiffchaff and Willow Warbler arrival dates. Territory mapping was conducted between 12 March and 20 May 2017. The study site was split into two sections (Figure 1) and each section was surveyed on alternate days. Surveys took place between dawn and dusk for a minimum of five hours each day, for six days a week (ensuring that the entire woodland was surveyed a total of three times each week). Recorded arrival dates are therefore accurate to 2–3 days. Newly arrived males and females were detected by walking at a slow pace (~1 mph) along woodland rides listening for songs and calls of both species. Newly arrived individuals were defined as being at least 20 m away from locations of previously detected individuals, to ensure no territory overlap occurred, using methods described by Rodrigues (1998). The date and co-ordinates of each newly arrived bird were recorded using a hand-held global positioning system (GPS) device.

Male Chiffchaffs and Willow Warblers are extremely vocal when defending a territory, making them easily detectable; therefore males were identified as singing individuals. Females of both species were less detectable and were only noticeable when gathering nest material, vocalizing, or being mate-guarded by a male. Consequently, the numbers of female Chiffchaffs are likely to be under-represented in the data, but the patterns of earlier arrival of males than females in the two species should be representative. Individual arrival dates were recorded for 82 male and 36 female Chiffchaffs, and for 17 male and 3 female Willow Warblers.

Colour-ringing and tracking individuals

Colour-ringing was used to monitor movements of individual birds with known arrival dates and identities throughout their breeding cycle, and to relate arrival dates to the timing of pairing and nesting. Attempts to catch and individually colour-ring individuals were made within one week of arrival, by deploying mist-nets at arrival locations with loudspeakers playing conspecific song and mixed *Phylloscopus* calls. Females of both species were not responsive to tape lures and were not targeted, but two females were caught. Sex was determined from the presence or absence of a brood patch (female) or cloacal protuberance (male) (Svensson 1992). A total of 56 Chiffchaffs (55 males and 1 female), and 11 Willow Warblers were colour-ringed (10 males and 1 female), and the GPS co-ordinates of subsequent locations of these colour-ringed individuals were used to measure individual consistency in territory occupancy over the duration of arrival surveys, and the frequency and scale of movement of individuals across the forest.

Measuring pairing, clutch initiation, and re-nesting dates

Paired males of both species were located by observing male mate-guarding behaviour before nesting, as described by Gil *et al.* (1999) and Rodrigues (1996), and pairing dates were defined as the date on which males were first observed mate-guarding a female. A total of 16 paired male Chiffchaffs and 2 paired Willow Warblers were recorded.

Searches for nests of both species were conducted by walking at a slow pace and listening for female calls. Located females were then followed for a minimum of 10 min and, if seen with nesting material, females were followed to the nest location. If the nest was not

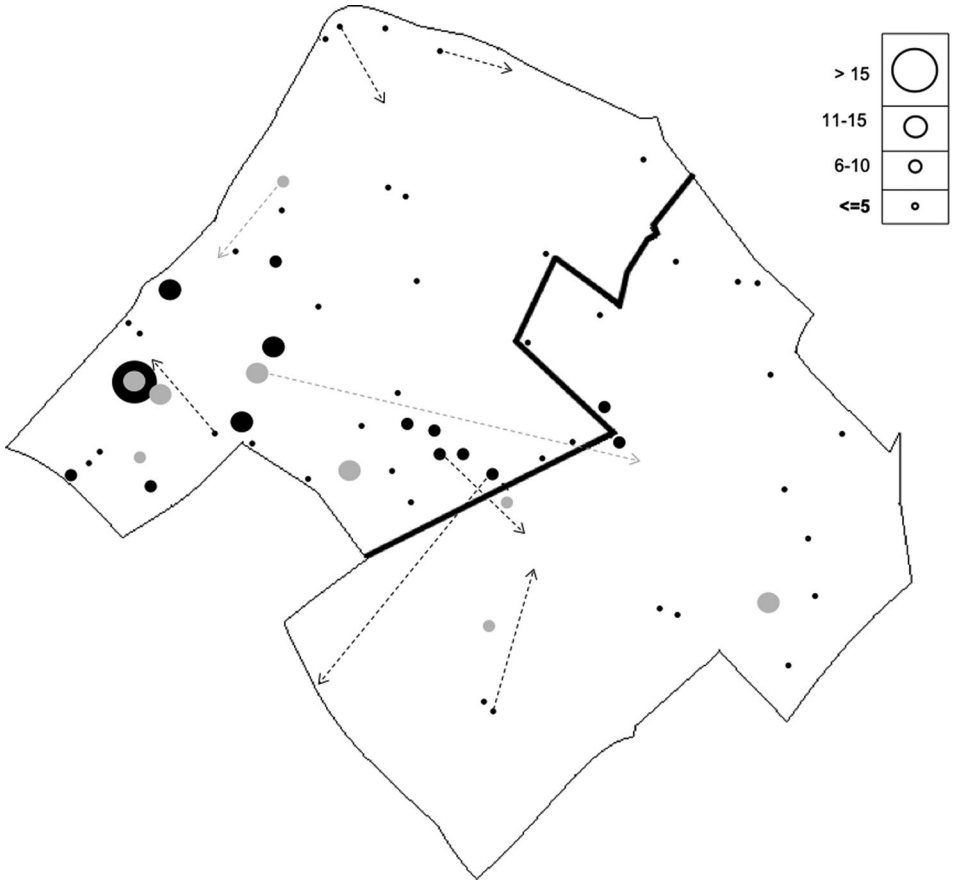

Figure 1. The locations at which individually colour-marked male Chiffchaffs (black circles, 54 individuals) and male Willow Warblers (grey circles, 9 individuals) were re-sighted in Foxley Wood. Circle sizes denote the number of times each individual was re-sighted, and arrows indicate movements (>30 m) by six male Chiffchaffs (black arrows) and two Willow Warblers (grey arrows). The black line separates the two sections of the woodland that were surveyed on alternate days.

located within 20 min, repeat visits to the same location were made on subsequent days to try and locate the nest. Once nest locations were confirmed (13 nests), repeat visits to each nest were made every three days to determine if the nest was active or not. Nests were classed as active if females were laying or incubating eggs (7 nests), or feeding hatched chicks or recently fledged young (6 nests).

For nests located before or during egg laying, clutch initiation dates could be calculated, as one egg is laid per day, followed by an incubation period of 13–14 days and a further 13–16 days from hatching to fledging (Ferguson-Lees *et al.* 2011, Rodrigues & Crick 1997). The four Chiffchaff nests found after the eggs had hatched were assigned an estimated clutch initiation of 14 days prior to discovery (the midpoint of a 14-day incubation period (7 days) + 7 days for egg laying), and the two Chiffchaff nests found at the fledging stage were assigned an estimated clutch initiation of 28 days prior to discovery (midpoint of a 14-day pre-fledging period (7 days) + 14 days incubation + 7 days egg laying). Re-nesting attempts were identified as belonging to a previously failed pair by identifying colour-ringed individuals.

Statistical analyses

Arrival dates (measured in Julian days) were recorded for 118 adult Chiffchaffs and 20 adult Willow Warblers. Only two male Willow Warblers subsequently paired, and thus relationships between arrival and breeding phenology were only explored statistically in Chiffchaffs (although Willow Warbler data are presented for comparison). All statistical analyses were carried out using IBM SPSS statistics 24 and R v. 3.4.2 (R Core Team 2017).

To explore differences in the weekly arrival of male Chiffchaffs and Willow Warblers and female Chiffchaffs, we fitted a binomial generalized linear model (GLM) in R (3.3.1). We modelled the proportion of birds present in each week (number of birds present, number of birds not yet present), as a function of week (0–10), species and sex (male and

female Chiffchaff and male Willow Warbler; too few female Willow Warblers were recorded for analysis). In order to account for over-dispersion in the weekly count data, we used a quasi-binomial error distribution.

A linear regression and Pearson correlation were then used to test associations between the arrival date of individual male Chiffchaffs and their subsequent (1) pairing date and (2) clutch initiation date. The timings of the three recorded Chiffchaff re-nesting attempts are also presented for comparison, but were excluded from the analyses.

Results

Of the 55 male Chiffchaffs and 10 Willow Warblers that were colour-ringed, 54 Chiffchaffs and 9 Willow Warblers were re-sighted on a total of 301 separate occasions during the study period (mean ± sd number of resightings of each individual = 4 ± 3; Figure 1). Of the 65 colour-ringed males, 88% of resightings were within 30 m of the ringing location. Only eight unpaired males (six Chiffchaffs and two Willow Warblers) were recorded further from ringing locations (at distances of 200–600 m; Figure 1), and these movements all occurred later in the Chiffchaff breeding season (after 20 April 2017). Given the high level of consistency of individual locations within the forest, arrival dates of 27 unringed male Chiffchaffs that were subsequently located were included in the analyses.

Arrival date differences between species and sexes

Across the 10-week survey period, numbers of both species increased most rapidly in the 3–4 weeks following first arrival (Figure 2), and significantly more male Chiffchaffs arrived than female Chiffchaffs and male Willow Warblers (Figure 2, Table 1). The mean (±se) number of Chiffchaffs arriving per week was 8.2 ± 2.7 (males) and 3.6 ± 1.5 (females), while the mean number of Willow Warblers arriving per week was 1.7 ± 0.8 (males) and 0.3 ± 0.1 (females). In both species, the first males arrived 3–4 weeks before the first females, and the weekly pattern of arrival varied significantly between male and female Chiffchaffs, and between male Chiffchaffs and male Willow Warblers (Figure 2, Table 1).

Associations between arrival date and breeding phenology

There was a strong, positive relationship between the arrival dates of 16 male Chiffchaffs and their subsequent pairing dates, with pairing typically occurring approximately two weeks after male arrival (Figure 3(a)). The two Willow Warbler males were paired by day 131 (11 May; 39 days after arrival) and 142 (22 May; 46 days after arrival).

In contrast to pairing, the timing of Chiffchaff clutch initiation was not related to male arrival date (Figure 3 (b)) and timing of estimated clutch initiation for first nests ranged from day 117 (27 April) to day 140 (20 May). The gap between male arrival and estimated clutch initiation ranged from 43 to 51 days (mean = 47 ± 4 se), and the gap between pairing and estimated clutch initiation ranged from 21 to 51 days (mean 32 ± 5 se). The average number of days between estimated clutch initiation of the three failed nesting attempts for which subsequent replacement clutches were recorded was 15, 29 and 39 days. Only 4 of the 13 Chiffchaff nesting attempts reached the fledging stage and no Willow Warbler nests were found.

Discussion

The timing of arrival of individual migratory birds on their breeding grounds can have important consequences for the subsequent phenology of the breeding season, but the nature of these associations is not well documented. Here we find that, despite early-arriving males tending to be paired before later-arriving males, early arrival did not result in earlier nesting for Chiffchaffs. However, many Chiffchaffs had already paired before the Willow Warblers had arrived, and Chiffchaff nesting was recorded approximately two weeks before the first paired Willow Warblers were recorded.

The arrival patterns of Chiffchaffs and Willow Warblers varied considerably across the 10-week survey period. Chiffchaffs began arriving approximately three weeks earlier than Willow Warblers and about 75% of Chiffchaffs had arrived before the first male Willow Warblers were recorded. The total number of Chiffchaffs (both males and females) recorded each week was consistently higher than the number of Willow Warblers (Figure 2). While Willow Warblers are more numerous than Chiffchaffs in the UK overall, numbers of Chiffchaffs breeding in south-east regions of the UK have historically been greater than numbers of Willow Warblers. These differences have been exacerbated by recent rapid declines in Willow Warbler abundance in these regions (Morrison *et al.* 2010, 2016a), while numbers of Chiffchaffs have increased (Harris *et al.* 2018, Morrison *et al.* 2013). Substantially more males than females were recorded in both species (Figure 2),

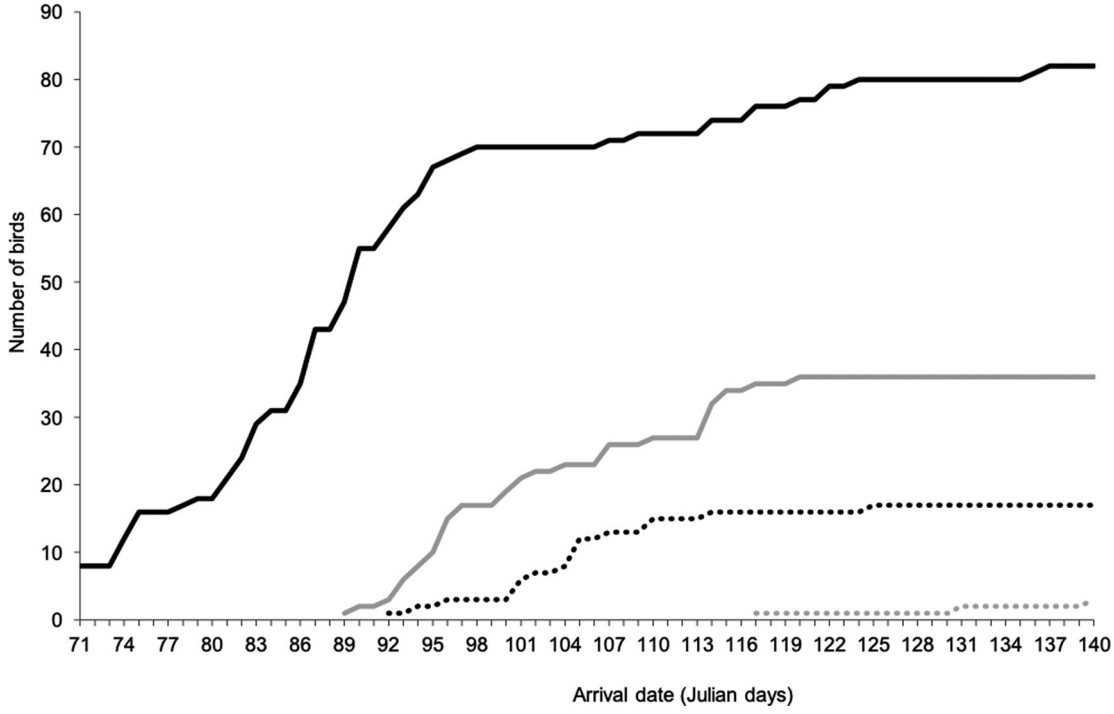

Figure 2. The daily arrival pattern (in Julian days) of male (solid lines) and female (dashed lines) Chiffchaffs (black) and Willow Warblers (grey) at Foxley Wood over the 10-week survey period from 12 March (day 71) to 20 May 2017 (day 140).

which is likely to reflect lower detectability of females, which do not sing and are typically very elusive during the breeding season. However, recent analyses have shown that male-biased Willow Warbler populations are common in areas where densities are low (Morrison *et al.* 2016b), and so unpaired males are likely in Willow Warblers, at least. In common with many migratory bird species (Morbey & Ydenberg 2001), the first males of both species arrived earlier than the first females. Female Chiffchaffs were first recorded approximately two weeks after males had been first recorded, but the subsequent cumulative pattern of arrival of both sexes was quite similar (Figure 2). By contrast, the first female Willow Warblers were recorded approximately three weeks after males had been first recorded, and very few additional females were subsequently recorded (Figure 2).

Table 1. Summary of a binomial generalized linear mixed model of weekly variation in the proportion of male and female Chiffchaffs (CC) and Willow Warblers (WW) arriving in Foxley Wood. All coefficients are presented on the logit scale. The intercept represents the proportion of male CC in week 0, and the coefficient estimates represent: Week = weekly change in the proportion of male CC arriving; CC(F) = mean difference between the overall proportion of male and female CC in week 0; WW(M) = mean difference between the overall proportion of male CC and male WW in week 0; Week*CC(F) = difference between the weekly change in the proportion of male and female CC arriving; Week*CC(M) = difference between the weekly change in the proportion of male CC and male WW arriving.

	Estimate	Std. Error	t value	*P*
(Intercept)	−1.70	0.24	−7.09	<0.001
Week	0.69	0.06	11.04	<0.001
CC(F)	−4.49	0.85	−5.31	<0.001
WW(M)	−7.22	1.92	−3.75	0.001
Week*CC(F)	0.65	0.18	3.64	0.001
Week*WW(M)	1.17	0.40	2.97	0.007

Early-arriving male Chiffchaffs paired earlier than those that arrived later, but males arriving in the first two weeks all paired around the same time, while later-arriving males tended to pair around 10 days later (Figure 3(a)). Thus, while earlier arrival in general can lead to earlier pairing, the earliest males were not necessarily the first to pair. No association between male arrival date and estimated clutch initiation was found (Figure 3(b)), suggesting that other factors may be involved in clutch initiation, such as resource availability or benefits associated with local breeding synchrony (Spottiswoode & Møller 2004, Stutchbury & Morton 1995). Willow Warblers arrived and paired later in the breeding season than Chiffchaffs, with the first Willow Warbler pairing observed 39 days after the first Chiffchaff pair had been recorded. No Willow Warbler nests were found and Chiffchaffs had already started nesting before the first male Willow Warbler was paired. Thus,

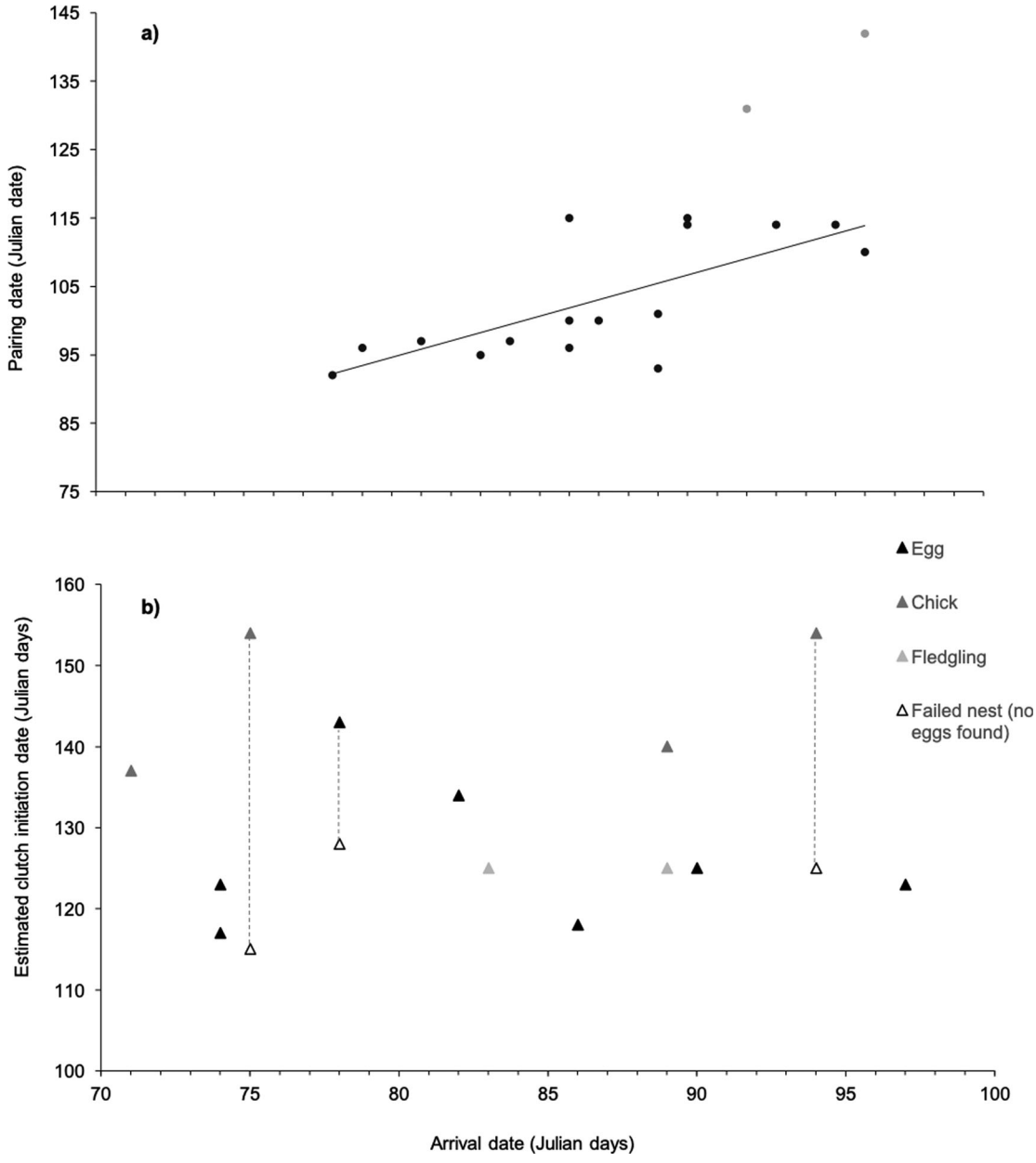

Figure 3. Relationships between arrival date and (a) pairing date for 16 male Chiffchaffs (black circles; $y = 1.2x - 1.714$, $R^2 = 0.51$, $P < 0.005$) and 2 Willow Warblers (grey circles) in Foxley Wood, and (b) estimated clutch initiation dates for 13 male Chiffchaffs (excluding three re-nesting attempts) ($r = -0.05$, $n = 10$, $P = 0.88$) for which nests were located at egg (black), chick (dark grey) or fledging (pale grey) stages (see methods for clutch initiation estimation at each stage). Dotted lines join failed feather-lined nests found before egg stage (open triangles) and replacement nests (not included in analyses) that were recorded in three Chiffchaff pairs.

Willow Warbler nesting, if it occurred, would be unlikely to begin until mid-late May, or early June (Figure 3(a, b)), a time that is likely to coincide with Chiffchaffs either completing a first nesting attempt or laying a replacement clutch following nest loss (Figure 3(b)).

There were three recorded re-nesting attempts (following nest failure) in Chiffchaff territories, and males that occupied these territories arrived on days 75, 78 and 94 of the survey period (Figure 3(b)). Chiffchaffs are multi-brooded, with the proportion of pairs attempting a second brood following a successful attempt varying between years (Rodrigues & Crick 1997), while Willow Warblers are typically single-brooded (Morrison *et al.* 2015b). Both species can have high nest failure rates because nests are located close to the ground and the contents are often predated (Rodrigues & Crick 1997, Stoate & Thomson 2000). The ability to re-nest following nest loss can have important consequences for annual productivity

(Jackson & Cresswell 2017), and can be particularly important in short-lived species in which population growth rates can be sensitive to recruitment rates (Sæther & Bakke 2000). A greater capacity for earlier-arriving Chiffchaffs to re-nest following nest loss could therefore mean that effects of high nest failure rates on overall productivity may be less severe than for later-arriving Willow Warblers.

In conclusion, while early male arrival facilitated early pairing in Chiffchaff, a short-distance migratory species, early arrival did not necessarily result in early breeding. However, Chiffchaff arrival was sufficiently early overall that pairs were able to begin nesting before the Willow Warblers had arrived and paired prior to breeding (Figure 3(a, b)). Willow warbler populations have declined severely in southern and eastern regions of the UK in recent decades, and levels of productivity in these regions are currently too low to allow these populations to recover (Morrison *et al.* 2016a). A lack of time to lay replacement clutches following nest loss could be an important contributor to these low levels of productivity, particularly if nest loss rates are high in the increasingly fragmented landscapes that characterize these regions. These results suggest that the time available to lay replacement clutches following nest loss could be a key benefit of early arrival, and could play an important role in determining levels of productivity in populations experiencing high rates of nest loss.

Acknowledgements

We thank the Norfolk Wildlife Trust and the British Trust for Ornithology for access and licensing permissions, respectively, and David Collins, Olivia Weekes, Alex Berryman, Harry Ewing, Charli Davies, James Cracknell and William Peden for assistance in the field. This work was undertaken as part of a University of East Anglia-funded Masters dissertation study.

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