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Reproductive consequences of the timing of seasonal movements in a nonmigratory wild bird population

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Abstract. Animal movement patterns, whether related to dispersal, migration, or ranging behaviors, vary in time. Individual movements reflect the outcomes of interactions between an individual's condition and a multitude of underlying ecological processes. Theory predicts that when competition for breeding territories is high, individuals should arrive at breeding sites earlier than what would otherwise be optimal for breeding in the absence of competition. This is because priority at a site can confer significant competitive advantages leading to better breeding outcomes. Empirical data from long-distance migrants support this theory. However, it has not been tested within the context of fine-scale movements in nonmigratory populations. We assessed the effect of arrival time at a breeding site on reproductive outcomes in an intensively monitored resident population of Great Tits (*Parus major*). The population was monitored passively, via passive integrated transponder (PIT) tag loggers, and actively, via catching, during breeding and nonbreeding seasons. We developed new capture–recapture–resight models that use both data types to model breeding outcome conditional on the unknown individual arrival times. In accordance with theory, individuals arrived at the woods synchronously in waves that were large at the beginning of the nonbreeding season and small toward the end, with very few arrivals in the intervening period. There was a strong effect of arrival time on the probability of breeding; the earlier an individual arrived, the more likely it was to successfully establish a nest that reached the incubation period. However, once nests were established, they had equal probabilities of failing early, regardless of arrival time. Finally, there was moderate evidence of a negative effect of arrival time on the probability of successfully fledging nestlings. These empirical findings are consistent with theoretical models that suggest an important role for competition in shaping fine-scale seasonal movements. Our capture–recapture–resight models are extensible and suitable for a variety of applications, particularly when the goal is to estimate the effects of unobservable arrival times on subsequent ecological outcomes.

Key words: arrival time; breeding success; capture–recapture–resight; Great Tit; Parus major; reproductive outcome; super-population; synchronous arrival; Wytham Woods, UK.

Introduction

Animal movement and dispersal patterns structure populations in space and time, and are thus fundamentally important for understanding many ecological and evolutionary processes (MacArthur 1972). However, the reproductive consequences of movement related behaviors are not well known. This is because a considerable number of internal and external factors act together to shape individual movement decisions (Matthysen 2011, Bonte et al. 2012). For seasonally breeding species, costs associated with nonbreeding seasonal movements can begin to accrue with the initial decision to move, or not, and continue to accumulate until breeding begins

(Clobert et al. 2009, Bonte et al. 2012). When competition for breeding resources is intense, theory predicts that arrival time at a breeding site should reflect the accumulation of these difficult-to-measure costs of movement (Kokko 1999). High-quality individuals are expected to arrive earliest, consequently gaining considerable reproductive benefits associated with priority at breeding sites (Kokko 1999).

Previous empirical work, primarily focused on seasonal, long-distance migrants, has supported this theory. Individuals that arrive at breeding sites early tend to be in good condition, are better competitors, find quality mates more easily, and have increased reproductive success, when compared to individuals that arrive later in the season (see, for example, Thornhill and Alcock 1983, Flood 1984, Michener 1984, Francis and Cooke 1986, Hill 1988, Carranza et al. 1990, Enstrom 1992, Grewal et al. 1993, Lozano et al. 1996, Dickerson et al.

Fig. 1. The location of data loggers (large circles) and nest boxes (small circles) in Wytham Woods, UK (latitude and longitude: 51.77, −1.34). Inset shows the location of Wytham Woods (star) within the British Isles.

2005, Gienapp and Bregnballe 2012). These trends are often attributed to higher quality individuals being better able to absorb costs associated with arriving earlier than what might, strictly, be optimal for breeding if there was no competition. By arriving early, these individuals may gain a substantial competitive advantage associated with prior occupancy of breeding territories.

The movement patterns of seasonally breeding nonmigratory species that compete for breeding territories are expected to show similar relationships (Kokko 1999). However, the effects of seasonally variable, fine-scale ranging patterns and dispersal on breeding outcomes in nonmigratory populations have rarely been empirically addressed. In nonmigratory species, early establishment at a breeding site could lead to better opportunities to compete for quality territories, to find a mate, to integrate socially, and to become familiar with the local environment. We thus predict that early establishment at a breeding area will be associated with positive reproductive outcomes.

Here we examined the relationship between the estimated time of arrival into a breeding population, whether following dispersal or seasonal movements, and reproductive success in a resident Great Tit (*Parus major*) population. Great Tits begin to defend breeding territories in late winter and subsequently rear offspring on those territories. There is considerable competition for territories, and site-based priority is a strong predictor of competitive outcomes (Krebs 1971, 1982). Breeding territoriality begins to break down after nestlings have fledged and individuals start to integrate into social flocks for the winter. These flocks can travel large distances relative to breeding territory size (e.g., >3 km straight-line distances relative to territory sizes

typically <2 ha in our system [Krebs 1971]). Dispersal takes place during this winter flocking period. This life history pattern is broadly similar to many other temperate passerine species.

We treated Wytham Woods, UK, a discrete 385-ha area of contiguous mixed woodland that is isolated from other woodlands by agricultural and urban landscapes, as our breeding site (Fig. 1). Great Tits at this site were monitored throughout the breeding and nonbreeding season both actively via catching, and passively via passive integrated transponder (PIT) tag loggers. We developed a capture–recapture–resight (CRR) modeling framework that allowed breeding-related parameters to be dependent upon the unknown arrival time of individuals at the study site. Specifically, we modeled the relationship between arrival time and the probability of (1) nest initiation (individuals identified at the onset of egg incubation), (2) early nest failure, and (3) fledging nestlings. These models allowed us to estimate key demographic parameters of the population conditional upon sampling effort and allowing for imperfect detection and trap effects.

METHODS

Data collection

Data were collected during both the nonbreeding season (NBS; 8 August to 10 March) and breeding season (BS; 12 April to 21 June) of 2011–2012, as part of the Edward Grey Institute's long-term study of the Great Tit population in Wytham Woods, Oxfordshire, UK. Data collection during our study period, relative to other years, was unique in two ways. First, we systematically sampled individuals throughout the NBS via mist-netting in a manner that ensured regular coverage of the woods. Second, we scanned nest boxes

during the night following the onset of incubation to detect PIT-tagged females incubating eggs early in the breeding season (see Plate 1). For these reasons, we focused our analysis on this single year.

During the NBS, individuals were sampled via both mist-netting and automated PIT-tag detection systems on $K = 32$ weekly sampling occasions. The mist-netting sessions occurred in 28 of the 32 weeks. Each session systematically covered several areas of the site. When caught, Great Tits were marked with a uniquely numbered metal ring in accordance with the British Trust for Ornithology's (BTO) banding (ringing) scheme or identified from a previously affixed ring. Every caught individual was also fitted with a PIT tag molded into a plastic leg ring (manufactured by IB Technology, Aylesbury, UK).

PIT-tag monitoring during the NBS occurred during 24 of the 32 weeks. PIT-tagged individuals could be resighted at 65 automated feeding stations placed on a stratified grid throughout the study site (Fig. 1). Stations consisted of bird feeders fitted with radio-frequency identification (RFID) antennae in place of the perch at two access holes (manufactured by Dorset ID, Aalten, Netherlands). When an individual lands on an antenna, its identity is transmitted to a data logger by the tag and stored with a time stamp. Feeding stations were programmed to make food available for two days a week to avoid them becoming a permanent attractant. Feeders were opaque so that birds could not assess food depletion and large enough that they did not empty during the brief periods that they were open.

Individuals were also monitored by both catching and PIT tags on three occasions during the BS. Great Tits in this system preferentially breed in nest boxes, and so, by providing an excess of nest boxes (>1200), we are able to monitor breeding attempts of the entire population (Perrins 1979). First, we attempted to detect roosting female birds at nest boxes immediately following the initiation of incubation (incubation stage) by scanning the outside of nest boxes at night with a hand-held PIT-tag reader. We considered female birds only in this study because they alone roost on nests during incubation and so can be detected much earlier in the breeding season than males. Subsequently, we attempted to capture females at the nest box using spring traps when their nestlings were between 7 and 11 days old (nestling stage). Nest failure between nest box scanning and adult catching was recorded. Finally, nests were revisited 20 days after nestlings hatched to determine fledging success (fledging stage). For our purposes, we defined fledging as successful if an individual successfully fledged at least one nestling.

In total, the data set considered consisted of 641 female birds. Four-hundred and nine of these were marked with PIT tags and rings prior to the study period. The additional 232 individuals were marked during the study period. With these data, we sought to model the effects of arrival time during the NBS on the probability of reaching the incubation stage, the nestling stage, and the fledging stage during the BS.

Model development

At the start of the study, birds could already be marked (M) with rings and PIT tags if they were caught or hatched in the woods in previous years, or unmarked (U) if they were new immigrants or avoided capture in previous years. The numbers of marked and unmarked birds available for detection are denoted N_M and N_U, respectively, with $N = N_M + N_U$ being the population size in the woods. During our study period each of the N birds could be detected during the NBS, the BS, both, or not detected at all.

We considered the population to be open to immigration and emigration/death and assumed that all N individuals present during the BS arrived during the NBS. Parameters to model the arrival, departure, and breeding behavior of the individuals, as well as the observation process are incorporated in our models. A schematic representation of these processes is given in Fig. 2, and definitions of the parameters are given in the legend.

The model, described in detail in Appendix A, builds on the work of Pledger et al. (2009), who modeled the probability of departure from a stopover site as dependent upon the unknown time of arrival at the site, and the Matechou et al. (2013a) model, which accounted for two types of sampling. The data collected during the NBS are modeled by extending the aforementioned models to account for trap effects in capture and resight probabilities. We allowed for capture and resight probabilities to be different for individuals that have already been caught or have used the feeders at least once during the study period, because individuals may learn to avoid mist nets or to identify open data loggers as food sources. The model has been motivated by the study of Great Tits, and hence, has been tailored to the sampling scheme used in the study, but it can be easily adjusted to different sampling schemes, both during the NBS and BS. The log-likelihood function was written in C and model fitting was performed in R (R Core Development Team 2013). We have calculated confidence intervals both asymptotically, using the asymptotic normal distribution of maximum likelihood estimators, and by using nonparametric bootstrap (Efron and Tibshirani 1994). The first approach is less time consuming, but the latter does not rely on asymptotics. All code and data are available in the online Supplement. Model performance is assessed in a simulation study presented in Appendix B.

Model selection

We chose to use a backward elimination model simplification strategy with Akaike information criterion (AIC; Akaike 1973) as a model selection criterion. All models considered have entry parameters that are fully time dependent, denoted by $\beta(t)$, which requires the

Nonbreeding season, NBS

Breeding season, BS
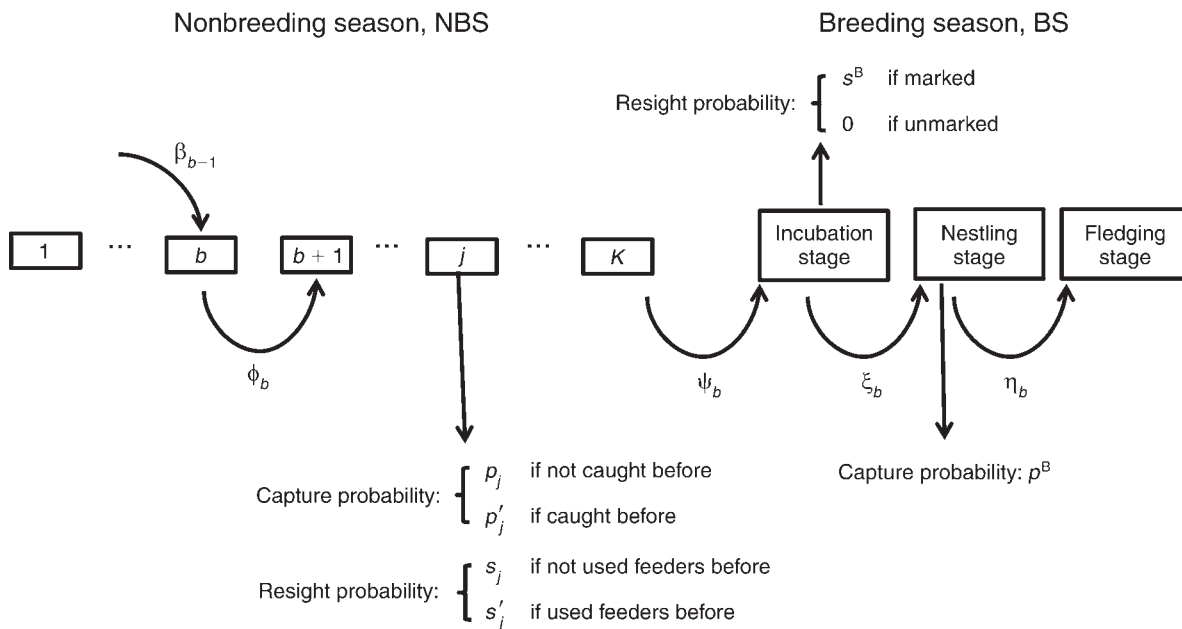

FIG. 2. Schematic representation of model parameters. The entry parameters, β, model the arrival of the individuals at the site. The proportion of the N individuals that are new additions to the population on sampling occasion b is denoted by β_{b-1} with $\sum_{b=1}^{K} \beta_{b-1} = 1$, where K is the number of sampling occasions during the nonbreeding season (NBS). The apparent survival parameters, ϕ, model the departure of the individuals from the site. The probability that an individual present on occasion b is also present on occasion $b+1$ is denoted by ϕ_b. Emigration, and of course death, are assumed to be permanent and apparent survival of breeding individuals is assumed equal to 1 during the breeding season (BS). Ellipses represent the fact that there are more boxes, i.e., samples, between the ones that are shown. Individuals that were newly arrived in week b, and are present at the end of the nonbreeding season, establish a nest that reaches the incubation stage with probability ψ_b. Subsequently, their nest reaches the nestling stage with probability ξ_b, and finally, conditional on having reached the nestling stage, they successfully fledge at least one nestling with probability η_b. An individual, present at the site on occasion j, that has not been previously caught during the study period, is captured with probability p_j. An individual, present at the site on occasion j, that has not previously used the feeders during the study period, is resighted with probability s_j. The corresponding probabilities for birds that have been caught and for birds that have used the feeders during the study period are p'_j and s'_j, respectively. The probability of detecting a marked bird that is in the incubation stage is s^B and the probability of capturing a bird that is in the nestling stage is p^B. Fledging success (fledging stage) can be assessed with probability 1 for all nests.

estimation of $K - 1$ parameters. Apparent survival probabilities are modeled as either fully time dependent, denoted by $\phi(t)$ or as constant, denoted by $\phi(c)$. Capture probabilities are expected to vary between the different weeks since the number of locations visited during each capture occasion (capture effort e_c), changed during the course of the study. The same holds for resight probabilities, since the number of feeders that were functioning each week (resight effort e_r), also varied. Therefore, all models considered have capture probabilities and resight probabilities, on the logit-scale, as functions of e_c and e_r, respectively, denoted by $p(e_c)$ and $s(e_r)$. If trap effects in capture/resight probabilities are not accounted for, then $p(e_c) = p'(e_c)$ and, correspondingly, $s(e_r) = s'(e_r)$. Finally, transition probabilities between stages during the BS (incubation stage ψ, nestling stage ξ, and fledging stage η) are either modeled using a logistic regression model with the unknown time of arrival, b, as the covariate ($\psi(b)$, $\xi(b)$, and $\eta(b)$), or are assumed common between all individuals ($\psi(c)$, $\xi(c)$, and $\eta(c)$).

To arrive at our final model, we systematically considered model simplifications, starting with the most complex model that allowed for entry parameters and

apparent survival to vary with time, $\beta(t)/\phi(t)$, trap effects in capture and resight probabilities, $p(e_c) \neq p'(e_c)/ s(e_r) \neq s'(e_r)$, and an effect of arrival time, b, on all breeding-related parameters, $\psi(b)/\xi(b)/\eta(b)$. We compared this model to all parameter simplifications, mentioned in the previous paragraph, in turn, and the model with the lowest AIC was retained and further systematic simplifications were subsequently considered. We continued this process until the model with the lowest AIC value was identified. The model selection steps are shown in Table C1 of Appendix C.

RESULTS

AIC model selection suggested that the top four models were approximately equally well supported. These models differ only in the way transition probabilities between nestling and fledging stages (ξ and η) are modeled. They gave very similar estimates and overlapping asymptotic 95% confidence intervals for all shared parameters (Table 1).

The model $\beta(t)/\phi(c)/p(e_c) = p'(e_c)/s(e_r) \neq s'(e_r)/\psi(b)/ \xi(c)/\eta(b)$ is the model with the lowest AIC value, if only marginally, and was thus selected for interpretation and

TABLE 1. Estimated parameters, together with 95% asymptotic confidence intervals in parentheses, obtained by the top models, according to Akaike information criterion (AIC).

Quantity of interest	Model			
	$\xi(b)/\eta(b)$	$\xi(c)/\eta(b)$	$\xi(b)/\eta(c)$	$\xi(c)/\eta(c)$
AIC	9309.8	9309.1	9310.1	9309.6
ν	48	47	47	46
$\hat{N}_M$	495.4	496.1	496.2	496.2
	(456.5, 537.6)	(456.9, 538.6)	(457.2, 538.5)	(457.1, 538.7)
$\hat{N}_U$	480.5	479.5	479.6	479.6
	(420.9, 548.5)	(420.1, 547.3)	(420.2, 547.6)	(420.2, 547.5)
$\hat{\phi}$	0.985	0.985	0.985	0.985
	(0.982, 0.988)	(0.982, 0.988)	(0.982, 0.988)	(0.982, 0.988)
$\widehat{intercept}$				
ψ	0.393	0.38	0.392	0.378
	(−0.05, 0.834)	(−0.059, 0.818)	(−0.049, 0.834)	(−0.061, 0.816)
ξ	1.214	1.422	1.215	1.422
	(0.779, 1.650)	(1.118, 1.725)	(0.780, 1.650)	(1.118, 1.726)
η	2.076	2.095	2.4	2.397
	(1.546, 2.605)	(1.580, 2.612)	(1.970, 2.823)	(1.970, 2.823)
$\widehat{slope}$				
ψ	−0.843	−0.864	−0.842	−0.863
	(−1.296, −0.390)	(−1.315, −0.414)	(−1.294, −0.390)	(−1.312, −0.414)
ξ	−0.288	…	−0.288	…
	(−0.755, 0.178)		(−0.753, 0.177)	
η	−0.522	−0.506	…	…
	(−1.136, 0.092)	(−1.103, 0.092)		
$\widehat{s^B}$	0.728	0.728	0.728	0.729
	(0.643, 0.799)	(0.644, 0.799)	(0.643, 0.799)	(0.644, 0.799)
$\widehat{p^B}$	0.376	0.375	0.376	0.375
	(0.317, 0.439)	(0.316, 0.438)	(0.317, 0.439)	(0.316, 0.438)

Notes: Model parameters are fully defined in Fig. 2. The numbers of marked and unmarked birds available for detection are denoted as N_M and N_U, respectively. These equally well-supported models only differ in the way in which transitions between the incubation stage to the nestling stage, and the nestling stage to the fledging stage are modeled. The number of parameters in each model is denoted by ν. All four models suggest that the probability of initiating a nest that lasts until the incubation stage is strongly dependent upon arrival time. The top model also suggests that the probability of fledging at least one nestling is dependent upon arrival time; however, this effect is considerably weaker. Ellipses indicate that the specific parameter does not exist in the model represented in that column.

its results are presented in detail. This model allows the probability of successfully breeding until the onset of incubation, as well as the probability of successfully fledging at least one chick for birds that reached the nestling stage, to depend on the time of arrival ($\psi(b)\eta(b)$).

Additionally, it allows for resighting probabilities at PIT-tag loggers associated with the NBS to depend on whether a bird had used the feeders before ($s(e_r) \neq s'(e_r)$). It also suggests that apparent week-to-week survival probabilities did not vary with time ($\phi(c)$), and that capture probabilities were not different after an individual had been captured for the first time during the study ($p(e_p) = p'(e_p)$). All subsequent confidence intervals presented are 95% nonparametric bootstrap confidence intervals derived by resampling with replacement the individual birds 100 times and refitting the model to each new data set.

Capture probability during the NBS was relatively low, with an average over the 28 weeks that capture took

place of 0.04 (standard deviation = 0.052). The intercept in the logistic regression model was −3.710 (−3.809, −3.569) and, as expected, the coefficient of the effect of capture effort was positive (0.723, CI = 0.658, 0.786). Though the probability of capturing a bird on any one week was low, due to the large number of sampling occasions and the high apparent survival probability, the probability of capturing a bird at least once is markedly greater. Resight probability during the NBS was considerably higher than capture probability (mean of estimates = 0.123, standard deviation = 0.006 for birds that had not used the feeders during the current study period and 0.661, standard deviation = 0.237 after birds had used the feeders at least once during the current study period). The two bird categories, those that have previously used the feeders and those that have not, had, as expected, different baseline resight probabilities, with intercepts in the logistic regression models of −1.938 (−2.081, −1.741) and 0.327 (0.179, 0.462). Interestingly, the effect of resight effort on resight probability was also

different for the two groups. For birds that had not used the feeders before, the slope was not different from 0 (−0.069, CI = −0.3627, 0.179), while for birds that had used them at least once, the slope suggests a strong positive effect of resight effort on resight probability (1.370, CI = 1.273, 1.509).

The cumulative sum of estimated entry parameters is shown in Fig. 3a. Most birds appear to have arrived before week 18, with a late group arriving shortly before the end of the NBS. The steep increases in the cumulative sums of the estimated entry parameters suggest that the birds arrive synchronously rather than at a constant rate.

The probability that a bird, present at the site at the end of the NBS, would successfully nest until the initiation of incubation (move to the incubation stage) decreased with arrival time, b (Fig. 3b). The confidence intervals become wider for late arrivals due to the smaller number of individuals arriving towards the end of the NBS.

The probability that a nest that reached the incubation period was still active 7–11 days after the eggs had hatched (transition probability from the incubation stage to the nestling stage) was $\xi = 0.806$ (0.757, 0.844). Finally, the probability that a nest that reached the nestling stage fledged at least one nestling, presented in Fig. 3c, was overall high and decreased slightly with arrival time, b. The upper bound of the 95% nonparametric bootstrap confidence interval is very close to 1 and roughly parallel to the x-axis, suggesting only a mild effect of arrival time.

DISCUSSION

The capture–recapture–resight models developed here extend concepts from the stopover model literature (Pledger et al. 2009, Matechou et al. 2013a, b) for use in resident populations. These models build upon the work of Schwarz and Arnason (1996), who represented additions to the super-population with entry parameters, as we have here, and share some similarities with models based upon an open robust design (Kendall et al. 1995, 1997). With this integrated modeling approach we could model the arrival pattern of individuals into the study population and model breeding outcomes as conditional upon the unknown times of arrival of the individuals at a breeding site.

←

(b) Estimated probability that a Great Tit, newly arrived at Wytham Woods in week b and present at the end of the nonbreeding season, establishes a nest that reaches the incubation stage ($\hat{\psi}_b$). (c) Estimated probability that a Great Tit, newly arrived at Wytham Woods in week b, moves from the nestling stage to the fledging stage (estimated probability of fledging at least one chick as a function of b conditional on having reached the nestling stage, $\hat{\eta}_b$). Dashed lines indicate the limits of 95% nonparametric bootstrap confidence intervals derived by resampling with replacement the individual birds and each time fitting the selected model to the data.
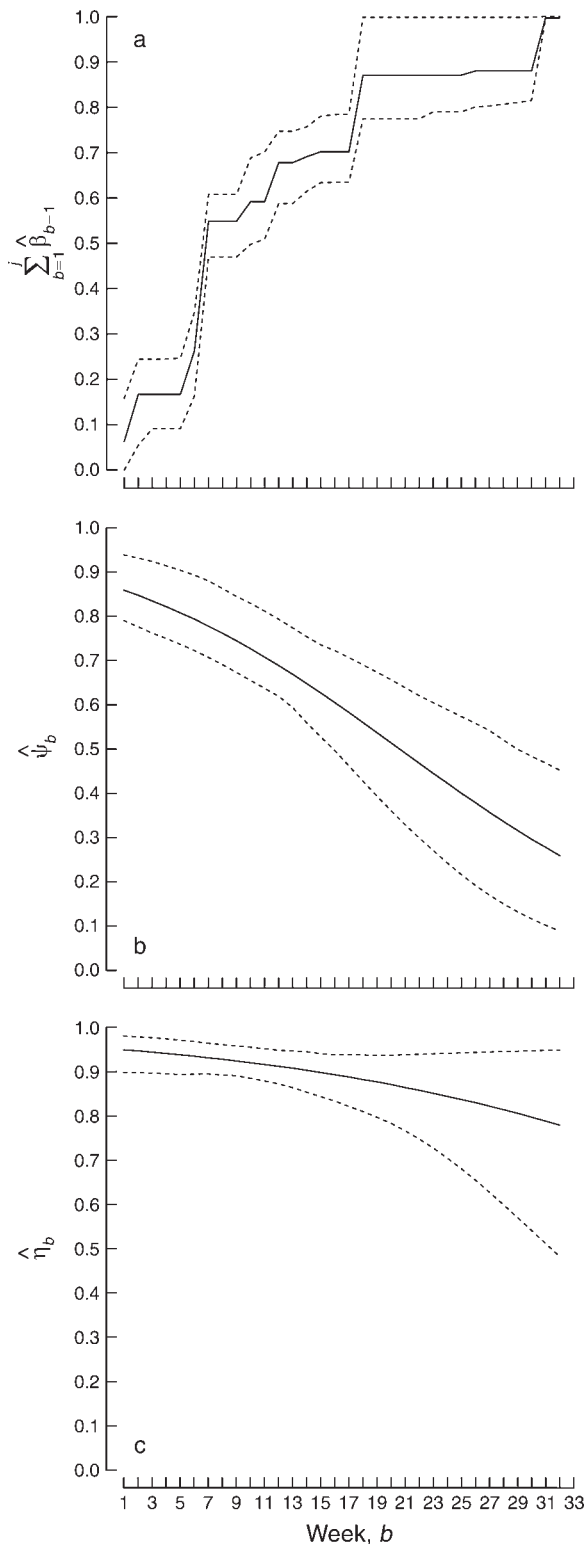
FIG. 3. Estimated parameters. (a) Cumulative sum of estimated entry parameters until week j ($\sum_{b=1}^{j} \hat{\beta}_{b-1}$) of Great Tits (*Parus major*) arriving at Wytham Woods, UK. Steep increases suggest synchronous arrivals. Parameter $\hat{\beta}_{b-1}$ denotes the proportion of birds that are estimated to be new arrivals at the breeding site in week b (week 1 is the first week of sampling).

PLATE 1. Adult (older than 1 year) female Great Tit (Y161635) brooding seven two-day-old chicks at box WB04 in Bagley Wood (UK) on 16 May 2013. Photo credit: Nicole Milligan.

Our model estimated that ~10% of all individuals that were available for detection over the course of the study period (the super-population) were present in the woods when monitoring began in early August. This corresponds to ~100 females, half of the number of resident individuals that are known to have subsequently bred. By mid-November just over 80% of the super-population had arrived. Between this time and late March very few individuals entered the population. The remaining 10–15% of individuals arrived during the final weeks of monitoring, prior to the BS. The shape of the cumulative sum of entry parameters (Fig. 3a) suggests that arrivals occurred in synchronous waves; large at the beginning of the NBS, followed by a period of stability, and then a final smaller wave at the end of the NBS. Week-to-week apparent survival probabilities were very high (>0.98), suggesting that once individuals arrived they tended not to leave the woods. Early arrival at the woods during the NBS was a strong predictor of successfully reaching the incubation stage of nesting. We found some evidence for weak effects of arrival time on fledging success.

The temporal patterns of these seasonal movements are, at least superficially, similar to a partial migration between natural woodlands for breeding and external sites, likely local towns and villages for overwintering. Our finding that a portion of the resident population leaves the woods after the BS and subsequently returns to the woodlands during the NBS fits well with previous observations from this and other populations (Odum 1942, Snow 1952, Gibb 1954, Perrins 1965, Lack 1966, Saitou 1979). Modeling the timing of these movements

showed that returning individuals arrive together with immigrants from other areas in two distinct, synchronous periods of arrival during the NBS. That arrival time was a strong predictor of successfully establishing a nest that reaches the incubation stage suggests that late arriving individuals may be of lower quality than earlier arrivals and year-round residents. Taken together, our findings might be explained by low-quality individuals tending to leave the woods for a more predictable food supply (e.g., garden feeders), being forced out due to competition, or incurring relatively higher costs of dispersal. Individuals arriving at the woods prior to the BS might then be expected to arrive according to their condition with later arrivals being less competitive for mates and territories. This could lead to the negative effects of arrival time on reproductive outcomes we have observed here. Similar positive effects of early arrival on aspects of breeding success have been found in long-distance migrants and these too have been attributed to individual quality and the costs of movements (e.g., Flood 1984, Francis and Cooke 1986, Hill 1988, Enstrom 1992, Lozano et al. 1996, Bêty et al. 2004, Gienapp and Bregnballe 2012). Full assessments of this proposed scenario would require additional data on condition and external movements of individuals.

The evolution of migration and arrival time strategies has received considerable theoretical attention. Particularly relevant to our findings, are models that have considered instances where competition for breeding sites is high, and competitive outcomes are closely associated with priority at a site (e.g., Kokko 1999, Sirot

and Touzalin 2014), as is the case for Great Tits (Krebs 1971, 1982). Kokko's (1999) model predictions in particular are strikingly similar to our empirical findings. She showed that when competition for breeding sites is high, leading to a risk of not obtaining a suitable territory, we should expect to see a large synchronous wave of individuals arriving earlier than what would be optimal in the absence of competition. These would tend to be high-quality individuals able to withstand survival costs of early arrival, and thus obtain reproductive benefits associated with prior occupancy advantages. Her model also predicts a second, later wave of lower quality "floater" individuals. These individuals arrive closer to their optimal breeding time, given their low quality. Breeding success among these later individuals was predicted to be much lower than earlier arrivals, as they would tend to settle on low-quality territories, rely on high-quality territories becoming vacant, or not settle at all. Finally, her model also predicts that competition can lead to the emergence of partial migration strategies as it should be beneficial for particularly high quality individuals to remain resident year-round. Our finding of two distinct periods of synchronous arrivals, a group of year-round residents, and a strong relationship between early arrival and breeding success provide empirical support for this model. This suggests that, in some instances, similar ecological processes may underlie seasonal movements of both migratory and nonmigratory species.

Our study differs from previous studies of long-distance migrants that found similar patterns in one important way: We found these patterns while examining female arrival times, whereas most other studies have focused on males. In long-distance migratory systems, males tend to arrive earlier than females, usually to establish and defend a territory. Females are thought to try to time their arrival closer to breeding. It is difficult to determine the cause of this difference with our data. Great Tits in this system are socially monogamous and there is evidence that pair bonds are, to a degree, maintained across the NBS (Psorakis et al. 2012). Thus, social tendencies during the NBS may then be responsible for this difference. Birds present in the BS will have arrived during the period that we designated the NBS, before individuals began defending territories. We hypothesize that establishment within social groups during the NBS plays a role in competitive outcomes and consequently, establishment on quality territories. Recent work demonstrates that Great Tits are particularly social and that these social relationships underlie many important ecological processes (e.g., Aplin et al. 2012, 2013). Some support for this contention can be found in previous work on Marsh Tits (*Poecile palustris*), which also form social flocks in winter. In this species, the timing of an individual's establishment in flocks, more so than both body size and age, predicted subsequent social dominance in competitive interactions (Nilsson and Smith 1988).

We also wish to emphasize that the models developed here are extensible and likely to be useful across a variety of scenarios and systems where the timing of movements might be expected to have ecological consequences. Capture–recapture–resight data collection, particularly using PIT tags to resight individuals, is becoming common practice for monitoring wildlife populations, e.g., fish (Prentice et al. 1990), amphibians, (Perret and Joly 2002), birds (Garroway et al. 2014), and mammals (Garroway et al. 2013). Incorporating both resight and recapture data allows for the estimation of population parameters using the much denser data associated with automated monitoring together with the additional information contained in data from physically captured individuals. Importantly, using both data types allows for some temporal demographic aspects of a system, particularly apparent survival and entry probabilities, to be estimated. With this information, one can then explore the ecological consequences of seasonal movements.

Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Caski, editors. Proceedings of the Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.

Aplin, L. M., D. R. Farine, J. Morand-Ferron, E. F. Cole, A. Cockburn, and B. C. Sheldon. 2013. Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). Ecology Letters 16:1365–1372.

Aplin, L. M., D. R. Farine, J. Morand-Ferron, and B. C. Sheldon. 2012. Social networks predict patch discovery in a wild population of songbirds. Proceedings of the Royal Society B 279:4199–4205.

Bêty, J., J.-F. Giroux, and G. Gauthier. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). Behavioral Ecology and Sociobiology 57:1–8.

Bonte, D., et al. 2012. Costs of dispersal. Biological Reviews of the Cambridge Philosophical Society 87:290–312.

Carranza, J., F. Alvarez, and T. Redondo. 1990. Territoriality as a mating strategy in red deer. Animal Behaviour 40:79–88.

Clobert, J., J. F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Dickerson, B. R., K. W. Brinck, M. F. Willson, P. Bentzen, and T. P. Quinn. 2005. Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. Ecology 86:347–352.

Efron, B., and R. J. Tibshirani. 1994. An introduction to the bootstrap. Chapman and Hall, New York, New York, USA.

Enstrom, D. A. 1992. Delayed plumage maturation in the orchard oriole (*Icterus spurius*): tests of winter adaptation hypotheses. Behavioral Ecology and Sociobiology 30:35–42.

Flood, N. J. 1984. Adaptive significance of delayed plumage maturation in male northern orioles. Evolution 38:267–279.

Francis, C. M., and F. Cooke. 1986. Differential timing of spring migration in wood warblers (*Parulinae*). Auk 103:548–556.

Garroway, C. J., J. Bowman, and P. J. Wilson. 2013. Complex social structure of southern flying squirrels is related to spatial proximity but not kinship. Behavioral Ecology and Sociobiology 67:113–122.

Garroway, C. J., R. Radersma, and C. A. Hinde. 2014. Perspectives on social network analyses of bird populations. Pages 171–183 *in* J. Krause, R. James, D. Franks, and D. Croft, editors. Animal social networks. Oxford University Press, Oxford, UK.

Gibb, J. 1954. Population changes of titmice, 1947–1951. Bird Study 1:40–48.

Gienapp, P., and T. Bregnballe. 2012. Fitness consequences of timing of migration and breeding in cormorants. PLoS ONE 7:e46165.

Grewal, P. S., S. Selvan, E. E. Lewis, and R. Gaugler. 1993. Male insect-parasitic nematodes: a colonizing sex. Experientia 49:605–608.

Hill, G. E. 1988. The function of delayed plumage maturation in male black-headed grosbeaks. Auk 105:1–10.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51:293–308.

Kokko, H. 1999. Competition for early arrival in migratory birds. Journal of Animal Ecology 68:940–950.

Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52:2–22.

Krebs, J. R. 1982. Territorial defence in the great tit (*Parus major*): Do residents always win? Behavioral Ecology and Sociobiology 11:185–194.

Lack, D. L. 1966. Population studies of birds. Clarendon Press, Oxford, UK.

Lozano, G. A., S. Perreault, and R. E. Lemon. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. Journal of Avian Biology 27:164–170.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York, New York, USA.

Matechou, E., B. J. T. Morgan, S. Pledger, J. A. Collazo, and J. E. Lyons. 2013*a*. Integrated analysis of capture–recapture–resighting data and counts of unmarked birds at stop-over sites. Journal of Agricultural, Biological, and Environmental Statistics 18:120–135.

Matechou, E., S. Pledger, M. Efford, B. J. T. Morgan, and D. L. Thomson. 2013*b*. Estimating age-specific survival when age is unknown: open population capture-recapture models with age structure and heterogeneity. Methods in Ecology and Evolution 4:654–664.

Matthysen, E. 2011. Multicausality of dispersal: a review. Pages 3–18 *in* J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock, editors. Dispersal ecology and evolution. Oxford University Press, Oxford, UK.

Michener, G. R. 1984. Age, sex, and species differences in the annual cycles of ground-dwelling sciurids: implications for sociality. Pages 81–107 *in* O. Murie and G. R. Michener, editors. The biology of ground-dwelling squirrels. University of Nebraska Press, Lincoln, Nebraska, USA.

Nilsson, J.-A., and H. G. Smith. 1988. Effects of dispersal date on winter flock establishment and social dominance in marsh tits *Parus palustris*. Journal of Animal Ecology 57:917–928.

Odum, E. P. 1942. Annual cycle of the black-capped chickadee: 3. Auk 59:499–531.

Perret, N., and P. Joly. 2002. Impacts of tattooing and PIT-tagging on survival and fecundity in the Alpine newt (*Triturus alpestris*). Herpetologica 58:131–138.

Perrins, C. M. 1965. Population fluctuations and clutch-size in the great tit. Journal of Animal Ecology 34:601–647.

Perrins, C. M. 1979. British tits. Collins, London, UK.

Pledger, S., M. Efford, K. H. Pollock, J. A. Collazo, and J. E. Lyons. 2009. Stopover duration analysis with departure probability dependent on unknown time since arrival. Environmental and Ecological Statistics 3:349–363.

Prentice, E. F., T. A. Flagg, and C. S. McCutcheon. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. American Fisheries Society Symposium 7:317–322.

Psorakis, I., S. J. Roberts, I. Rezek, and B. C. Sheldon. 2012. Inferring social network structure in ecological systems from spatio-temporal data streams. Journal of the Royal Society Interface. http://dx.doi.org/10.1098/rsif.2012.0223

R Core Development Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Saitou, T. 1979. Ecological study of social organization in the great tit, *Parus major* L., 3: Home range of the basic flocks and dominance relationship of the members in a basic flock. Journal of the Yamashina Institute for Ornithology 11:149–171.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. Biometrics 52:860–873.

Sirot, E., and F. Touzalin. 2014. Temporal patterns of arrival from migration as a response to competition for breeding space. Journal of Avian Biology 45:109–112.

Snow, D. W. 1952. The winter avifauna of arctic Lapland. Ibis 94:133–143.

Thornhill, R., and J. Alcock. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Massachusetts, USA.

Supplemental Material

Ecological Archives

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