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# Choice of model and re-nesting probability function influences behaviour of avian seasonal productivity models and their demographic predictions

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Measuring seasonal productivity is difficult in multi-brooded species without labour-intensive ringing studies. Individual-based (IB) models have been used to estimate seasonal productivity with no direct knowledge of number of nesting attempts, but they are often based on simplified re-nesting probability ($\varphi_R$) step-functions instead of observed or more biologically plausible ones. We present a new, open-source IB seasonal productivity model parameterized from studies of Black Redstart *Phoenicurus ochruros* and Yellowhammer *Emberiza citrinella*. We examined how the $\varphi_R$ function shape (empirical versus simplified) influenced (1) model performance, (2) re-nesting compensation and (3) population-level predictions of a simulated management intervention. Population-level predictions were made only for Yellowhammer as we had more detailed demographic data, such as survival rates, available. Pattern-oriented modelling revealed that IB models produced realistic within-population distributions of breeding parameters, and those specified with an observed or empirically derived $\varphi_R$ function generally outperformed those specified with simpler step functions. Strength of re-nesting compensation differed depending on the $\varphi_R$ function used. For Yellowhammers, type of $\varphi_R$ function in IB models marginally influenced population-level predictions of a simulated management intervention (potential population growth rate increased between 23% and 29% relative to no management intervention). In contrast, a simple deterministic productivity model, which did not simulate re-nesting compensation, predicted a 41% increase in potential population growth. At a population level, choice of $\varphi_R$ function may have less influence on IB model predictions, but choice of model itself (IB versus deterministic) may have substantial impact. We discuss how more biologically plausible $\varphi_R$ functions might either be observed directly, derived from nest data, or estimated from proxy information such as moult or brood patch changes.

**Keywords:** agent-based modelling, Black Redstart, individual-based modelling, multi-brooded, passerine, pattern-oriented modelling, repeat clutch, simulation, Yellowhammer.

The demographic parameters of productivity, survival and dispersal ultimately determine local avian population trends (Newton 1998). Their measurement is essential in bird conservation, for diagnosing

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proximate causes of population declines (Robinson *et al.* 2004) and for testing responses to management (Bolton *et al.* 2007). When considering productivity, it is ultimately the productivity per female per season that is required for demographic simulation or quantification of individual fitness (Green 2004) (or per male in polyandrous species). Many bird species have a long breeding season relative to the length of one nesting cycle and often attempt to produce multiple broods each season (Newton 1998, Green 2004, Weggler 2006). Direct measurement of individual seasonal productivity can be time-intensive and error-prone (Ricklefs & Bloom 1977). Monitoring individually marked females through a whole season is possible (e.g. Browne & Aebischer 2004, Kershner *et al.* 2004) but labour-intensive, particularly where potential nest-sites are abundant (Green 2004). For many researchers, such methods may be logistically impossible (Cornulier *et al.* 2009, Etterson *et al.* 2011). Unfortunately output per attempt and other indices may correlate poorly with seasonal productivity (Anders & Marshall 2005).

Instead, researchers have often used modelling to estimate seasonal productivity from incomplete data (Etterson *et al.* 2011). Various time-explicit models that dynamically link separate breeding parameters have been used (reviewed by Etterson *et al.* 2011). These include individual-based stochastic simulation (Powell *et al.* 1999), partial differential equations (Pease & Grzybowski 1995) and Markov chains (Etterson *et al.* 2009). Such dynamic models can be superior to deterministic models (that estimate productivity from estimates of output per attempt and the average number of attempts made) for at least three reasons. First, there is an acknowledged paucity of accurate data on number of attempts for many bird species (Siriwardena & Robinson 2002, Anders & Marshall 2005) and many nest studies are likely to underestimate this parameter (Pease & Grzybowski 1995, though see Cornulier *et al.* 2009 for an advance in indirect measurement). Secondly, they can be time-explicit, allowing consideration of intra-seasonal temporal variation in breeding parameters. Thirdly, they are capable of simulating 're-nesting compensation', which occurs because failed attempts 'use' fewer of the limited number of breeding season days available than successful attempts. Birds that fail may be able to make more attempts than those that are successful (Pease & Grzybowski 1995). Re-nesting compensation is expected to dampen the effect of inter-individual or inter-population variation in nest success on seasonal productivity (Nagy & Holmes 2004) and means that assuming a fixed number of attempts is ultimately biased (Pease & Grzybowski 1995). Dynamic models can address the lack of information on number of attempts by constraining it individually and indirectly via a distribution of 'quitting dates' (Pease & Grzybowski 1995, Mattsson & Cooper 2007, Etterson *et al.* 2009).

Quitting of breeding within a season is an active process (i.e. it is not solely defined by the cessation of nesting), as can be seen by post-breeding moult activity whereby females begin a moult during/after post-fledging care of their final brood, constraining further energetic investment in breeding (Newton 1999). Quitting dates can vary widely between individuals. For example, Black Redstarts *Phoenicurus ochruros* made as few as one failed attempt or as many as three successful attempts (Weggler 2006) and post-breeding moult in Eurasian Bullfinches *Pyrrhula pyrrhula*, which begins soon after their last attempt, varied across 7–11 weeks per season (Newton 1999). The complement to unity of the probability of a bird quitting the season ($\varphi_Q$) after an attempt is the re-nesting probability ($\varphi_R$; i.e. $\varphi_Q + \varphi_R = 1$).

Dynamic seasonal productivity models have previously used relatively simplistic assumptions about $\varphi_R$ (or equivalently $\varphi_Q$) that may not reflect its natural variation. For example, Pease and Grzybowski (1995) used a function assuming $\varphi_R = 1$ until the point when 50% of birds would cease to re-nest, then stepping to 0. Mattsson and Cooper (2007) used a function assuming a fixed mean $\varphi_R$ until the last known laying date observed from the population then stepping to 0. As recognized by the authors, neither approach seems biologically intuitive. Pease and Grzybowski's (1995) approach does allow for a time-variable $\varphi_R$ function but they used a simplified version in acknowledgement that such data are rarely available, and Mattsson and Cooper (2007) suggested a time-variable $\varphi_R$ as a future development. In study species where data are available on the propensity to re-nest following a given number of nesting attempts, attempt-variable $\varphi_R$ functions (i.e. $\varphi_R$ depends on if the subsequent attempt would be the second, third, etc.) have been used in seasonal productivity models: for Wood Thrushes *Hylocichla mustelina* and American Redstarts *Setophaga ruticilla* in Powell and Knutson (2006), and for Ring-necked Pheasants *Phasianus colchicus* in Matthews *et al.* (2012). However, the problem remains that such data are rarely available to investigators for many study species.

Beintema and Muskens (1987) predicted that $\varphi_R$ would be 1 early in the season and must fall to 0 at the end of the season, but suggested that the shape of the function is hard to estimate. A method that can estimate this shape, without the need for resource-intensive monitoring of marked birds through a whole season (e.g. Weggler 2006), would make such functions more widely available. As a result, models including empirically derived time-variable $\varphi_R$ functions have the potential to widen the functionality of seasonal productivity models by improving how they account for individual variation in quitting dates.

In this study, we present an open-source individual-based seasonal productivity model that can include a time-variable $\varphi_R$ function. Using two relatively data-rich study populations (Black Redstarts and Yellowhammers *Emberiza citrinella*) we obtained or constructed empirical re-nesting probability functions, and from those generated two comparable simpler step functions similar to those used in previous individual-based productivity model studies. We then ran the model for each species and $\varphi_R$ function combination, with three principal aims: (1) to use pattern-oriented modelling to assess the impact of the $\varphi_R$ function on model performance against real data; (2) to examine the impact of the $\varphi_R$ function on how the model simulates re-nesting compensation; and (3) for Yellowhammers only (for which other demographic data were available), to assess the impact of the $\varphi_R$ function on population-level predictions of a simulated management intervention. For the latter, we also compare the individual-based model to a simpler deterministic seasonal productivity model for reference. Finally, we discuss how researchers might extract more biologically realistic re-nesting functions from populations to improve the functionality of seasonal productivity models, and we provide some examples. The overall aim is to provide ornithologists with a greater range of tools for simulating re-nesting behaviour and so providing potentially more accurate estimates of seasonal productivity.

## METHODS

### Study populations

To assess the impact of choosing different $\varphi_R$ functions, we used data from two intensive studies of bird reproduction: one involving individually colour-ringed Black Redstarts (Passeriformes, Muscicapidae) in a small rural community in Wallis, Switzerland (Weggler 2006), and the other on Yellowhammers (Passeriformes, Emberizidae) on three close-proximity lowland farms in Leicestershire, UK (White *et al.* 2014). Both species are typically monogamous, with males establishing breeding territories, and can be described as ‘multi-brooded’ (i.e. a species that has the ability to have multiple broods in a season, even if not every individual does so; Snow & Perrins 1997).

There are very few datasets where individually marked individuals of a multi-brooded species have been followed through their entire breeding season such that the actual $\varphi_R$ function can be observed. Indeed, even where females are radio-tagged, logistical constraints mean that it can be difficult to locate second attempts (Kirby *et al.* 2019). However, Weggler (2006) colour-ringed 157 female Black Redstarts during 1994–2004, combining this with intensive nest finding (379 nests), such that there was high confidence that most nesting attempts, even early failed ones, were located.

The study of Yellowhammers took place between 1995 and 2007 as part of a larger study looking at the impacts of agricultural and game management on wild bird populations (Stoate *et al.* 2015). Adults were not individually marked, although territory-mapping was carried out in some years. A total of 732 nests were located and monitored; it was never intended that these would represent all nesting attempts made, but rather they would be a representative sample.

The Black Redstart study was selected to primarily assess the impact of the $\varphi_R$ function on model performance, as we had detailed data about breeding parameters recorded directly and independently of the modelling. Such data were not directly available for the Yellowhammer population as it was not intensively monitored using colour ringing.

The Yellowhammer study was, on the other hand, primarily selected to assess the consequences of $\varphi_R$ function on population-level predictions, as Yellowhammers are an extremely well-studied species on UK lowland farmland, in part in response to large-scale declines linked to agricultural intensification (Bradbury *et al.* 2000). As such, for Yellowhammers it was easier to parameterize a population model with demographic parameters specific to Great Britain. To our knowledge, no such data were available for Black Redstarts on mainland Europe. In addition, while other nest datasets could potentially be used for this type of assessment (such as from the British Trust for Ornithology's Nest Record Scheme), 732 nests of a single species within a very restricted geographical area represented a large sample size from a population experiencing similar local environmental conditions. Furthermore, for this Yellowhammer population we had some territory mapping data, which allowed us to assess our approach to estimating $\varphi_R$ functions for the population, discussed below.

## An individual-based re-nesting model

The model is based on, and follows a similar approach to, previous dynamic re-nesting models (Beintema & Muskens 1987, Powell *et al.* 1999, Mattsson & Cooper 2007). The model was originally generated and tested (validation, extreme conditions and sensitivity analysis) in Microsoft Excel (White 2009), then moved to NetLogo (Wilensky 1999) for ease of use and enhanced adaptability to other species/functions by other researchers. A link to the model itself, which also contains a detailed model description and example datasets, is given at the end of this article. NetLogo is a multi-agent programmable modelling environment that is free to download (https://ccl.northwestern.edu/netlogo/index.shtml).

Briefly, the model is individual-based and simulates the breeding season of a female, with each female time-limited by stochastic selection of (1) a start-date from a specified normal distribution of initial first-egg dates and (2) a quitting date, which was determined by, at the end each attempt, referring to a vector of re-nesting probabilities ($\varphi_R$; specific to day-in-season), which would decide whether the female either ceased breeding or made a subsequent attempt. Within that season, there are various other stochastic processes based on empirical probabilities and distributions, such as clutch size, daily survival probability of a nest (separately for egg and nestling stages), the proportion of eggs laid that hatch if hatching is reached, and the proportion of hatched chicks that fledge if fledging is reached. In addition, there are some constants such as duration of nest building, duration of laying and incubation, duration of provisioning, and inter-attempt intervals. The constants have the potential to be varied, but sensitivity analysis suggests that they do not impact model outputs substantially (White 2009).

## Developing re-nesting probability functions

To achieve aims (1), (2) and (3) we compared simple $\varphi_R$ functions of the type that have been used in previous models (in the absence of a more biologically plausible function) to empirical $\varphi_R$ functions that were more representative of real populations.

For the Black Redstart, whose population was intensively colour-ringed and monitored, we in fact had a true re-nesting probability ($\varphi_R$) function (fig. 2 in Weggler 2006), which we then used within the individual-based re-nesting model. As this is not typically available to investigators, we also reduced it to two simpler step functions analogous to those of Pease and Grzybowski (1995) (assuming $\varphi_R = 1$ until the point when 50% of birds would cease to re-nest, then stepping to 0), which for brevity we call the 'high step' function, and of Mattsson and Cooper (2007) (assuming a fixed mean $\varphi_R$ until the last known laying date observed from the population then stepping to 0), which we call the 'low step' function. The three Black Redstart $\varphi_R$ functions are shown in Figure 1a.

Because our Yellowhammer population was not colour-marked, nor as intensively studied, we took a novel alternative approach to obtaining the three different $\varphi_R$ functions. We first estimated an empirically derived $\varphi_R$ function as closely as feasible representing the real re-nesting probability function of the population. This involved use of encounter histories of nest initiations in assumed breeding territories and adaptation of a mark–recapture modelling approach (see Supporting Online Information, Appendices S1 and S2 for details). From this empirically derived $\varphi_R$ function, we also then derived simpler high step and low step functions, as for Black Redstart (see Supporting Online Information, Appendix S1). The three Yellowhammer $\varphi_R$ functions are shown in Figure 1b.

## Analyses

The framework for our analysis is outlined in Figure 2 to aid understanding. Capital letters in subheadings below match to those in the 'Analyses' column in Figure 2.

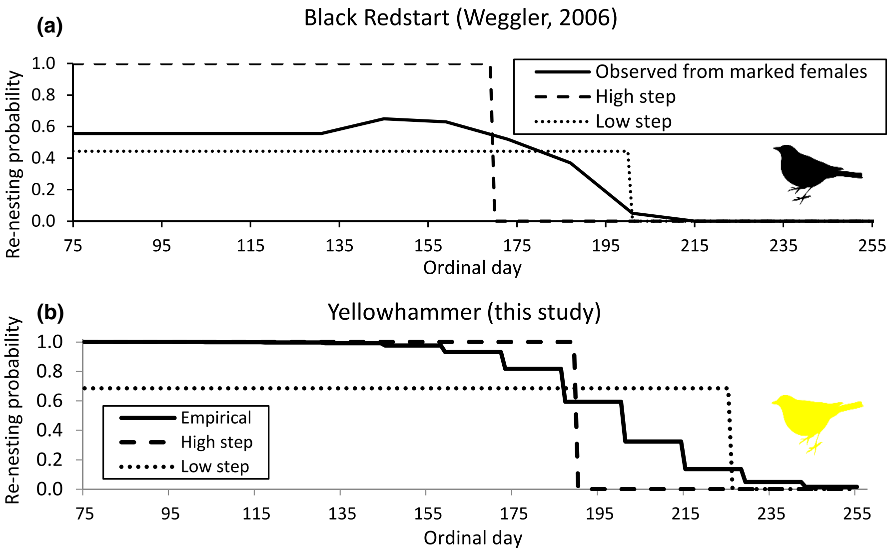

**Figure 1.** Re-nesting probability functions tested in this study for (a) Black Redstarts and (b) Yellowhammers. We compared the impacts of three different potential re-nesting probability functions on model performance of a stochastic simulation model (see text). Ordinal day indicates day in year where 1 = 1 January, ignoring leap years.

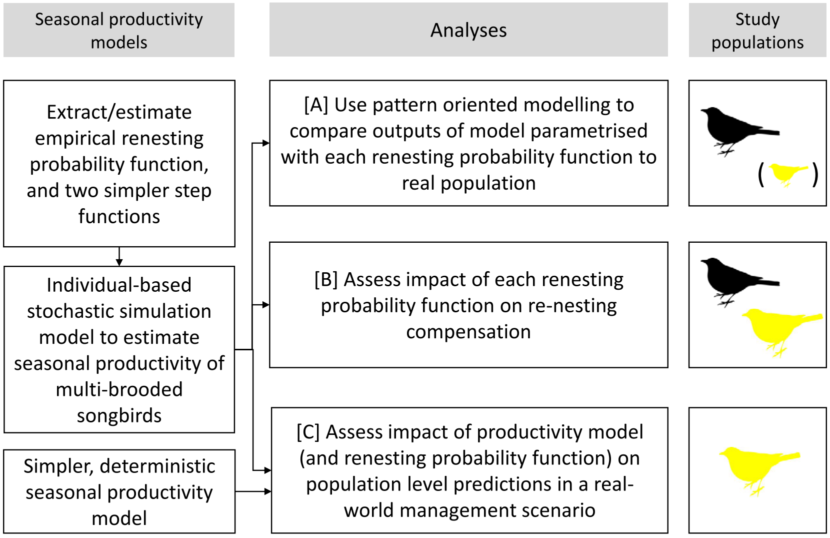

**Figure 2.** Framework of study to assess the impact of choice of re-nesting probability function on the performance of individual-based seasonal productivity models. Letters in square brackets indicate the Methods/Results sections that describe those analyses. Bird symbols indicate study populations used for model parameterization and validation/assessment: black/dark represents Black Redstarts in Switzerland, yellow/light represents Yellowhammers in Great Britain. Yellowhammers are shown in parentheses for analysis A because they were only subjected to a smaller pattern-oriented modelling procedure.

### *[A] Using pattern-oriented modelling to assess performance of the re-nesting model*

For an individual-based re-nesting model to be useful for researchers it needs to be able to simulate the nesting season of a population and produce realistic outputs in terms of seasonal productivity (chicks produced per female per season). Pattern-oriented modelling (POM) is a strategy for comparing models with empirical patterns. It can be used to balance a model's level of complexity and help to capture the processes in the system necessary for addressing the purpose of that model (Gallagher *et al.* 2021). Patterns can be drawn from different levels of the ecological hierarchy (Gallagher *et al.* 2021): because the re-nesting model used here is a single-species system with no direct environmental/abiotic processes, we drew patterns from the 'individual' and 'population' levels. POM was primarily carried out on the Black Redstart system because the author of Wegler (2006) provided us with the study's raw dataset.

We used the raw datasets to both parameterize our model and derive individual/population patterns, but we avoided circular logic by using different parameters in model parameterization to those in the POM exercise. Input parameters used in the model (constants or distributions) are given in Supporting Online Information, Appendix S3. In contrast, patterns used in POM were emergent effects from the system/model that were independent of those input parameters and for which equivalent data from the study population were available for comparison. For Black Redstarts these were: (1) distribution of nest initiations over time, separated by attempt (first attempt, second attempt, etc.); (2) clutch initiation period (time span between 10th and 90th centiles of clutch initiation dates across all attempts); (3) mean number of attempts; (4) relative frequency of number of attempts (percentage of birds making one attempt, two attempts, etc.); and (5) mean seasonal productivity (fledglings per female per season). For the less intensively studied Yellowhammer, we were only able to compare (1) the distribution of nest initiations over time (but not separated by attempt, as this was unknown in the study population) and (2) clutch initiation period.

Between-female variation in output parameters is a key feature of an individual-based model because we know that there can be a large variation between females in real breeding populations (discussed above), and this variation between females allows emergent effects such as re-nesting compensation. As such, we also compared measures of variation (quantified by the standard deviation, sd) between the observed and simulated parameters, above. For seasonal productivity and number of attempts, we used the simple sd from all female-seasons. Because clutch initiation period is specific to simulated population not to female-season, there is a single value per simulation. So, to estimate a measure of variation of clutch initiation period we carried out 10 000 bootstrap samples with replacement and estimated its sd. For relative frequency of number of attempts, the distribution is multinomial (percentage of one, two or three attempts, respectively) so instead of sd we estimated its multinomial standard error (se). This was estimated from the observed Black Redstart population only ($n = 226$ female seasons) because for the simulation data the se would be influenced by sample size, and we show below with other outputs that se would tend to zero with increasing sample size.

For POM and subsequent analyses discussed below, each simulation was run for 10 000 female-seasons. This value was selected initially as an arbitrarily large number that would not take too much processing time in NetLogo. However, we carried out an assessment to check that 10 000 runs were sufficient to offer high precision in model outputs, which is described in detail in the Supporting Online Information, Appendix S4. This assessment showed that for multiple independent simulations specified with the same input parameters, key model outputs (mean of seasonal productivity) and emergent distributions (sd of seasonal productivity, and relative frequency of number of attempts per female) reached constant values with high precision after 10 000 runs. The analysis also demonstrated what would be predicted arithmetically, that since se has sample size as a denominator, then as the number of female-seasons in a simulation increases, the se of the estimated mean will tend to zero. Indeed, at 10 000 female-seasons the se of seasonal productivity was just 0.03 chicks per female per season (c. 0.5% of the mean). In contrast, the sd of seasonal productivity remains consistent as the number of simulated female-seasons increases after several thousand. As such, outputs such as mean and sd of seasonal productivity and number of attempts from simulations with 10 000 runs can be considered as expected values from the model, given the input.

For this POM approach, most patterns were compared qualitatively/visually (a recognized approach in POM: Gallagher *et al.* 2021) as only one value was available for the actual population and for each of the three simulations per species. However, for distributions of first egg dates, as well as a visual comparison, we also conducted a Kolmogorov–Smirnoff test, with the null hypothesis that the cumulative distributions were drawn from the same pattern. This test has the benefit that it can be used where the two distributions have different resolutions (for Black Redstart nest initiations were only available in 10-day windows, and for Yellowhammers in 5-day windows, whereas for both species the model outputs categorized nest initiations per ordinal day, i.e. where 1 January is day 1 etc.). Summary statistics and the Kolmogorov–Smirnoff tests were carried out in R (R Core Team 2015).

### [B] How does the re-nesting probability function influence re-nesting compensation?

Because re-nesting compensation is an emergent property of the fact that failed attempts take, on average, less time than successful attempts and females have the ability to re-nest following failure, we would hypothesize that the form of the $\varphi_R$ function used (which influences when females finish nesting for a season) would in turn influence how a model simulates re-nesting compensation. Re-nesting compensation can be observed within a simulated model by running the model across a range of values of nest success and viewing the effect on mean numbers of attempts made per female. If re-nesting compensation is operating, then we would expect a negative relationship (as plotted in Flint *et al.* 1998). The strength and form of this relationship is also important, as it would determine the extent to which a model simulates the 'dampening' effect of re-nesting compensation on variation in nest success and may have knock-on impacts for population modelling.

To view re-nesting compensation, we ran each of the three Black Redstart and three Yellowhammer models for 10 000 females 10 times, where each time nest success was fixed at values within 10% and 100% inclusive, in 10% intervals. In practice, this had to be done by assuming constant daily survival probability between egg and chick stages and then varying those constants to achieve those nest success values, as the model assesses nest survival probability at the scale of the day-within-nest cycle rather than the nest cycle. For each nest success value, we extracted the mean number of attempts across the 10 000 females and plotted these against nest success, as per Flint *et al.* (1998).

### [C] What is the knock-on effect when population modelling?

If individual-based models simulate re-nesting compensation as an emergent effect, then it should dampen the effect of any variation in nest success on seasonal productivity, and potentially then on population growth, depending on presence of density-dependent processes. In turn, if the re-nesting probability function itself modifies the strength or shape of re-nesting compensation of a model, then the function used could influence predicted demographic effects of any changes in nest success. This might be important when predicting, for example, the effect of an anthropogenic impact on nest success at a population level, such as the impact of invasive rat control on Mauritius Olive White-eyes *Zosterops chloronothos*, which was predicted to improve nest success and potential population growth rate (Maggs *et al.* 2015). To investigate to what extent the use of a stochastic individual-based productivity model (and further what re-nesting probability function that model used) influenced population-level predictions in a real-world management scenario, we used the Yellowhammer study system. The Yellowhammer system was used because it was easier to obtain other demographic parameters based on the same species in the same country, because Yellowhammers have been widely studied in the UK. This was not the case for Black Redstarts in Switzerland. The management scenario involved the impact of predator removal on Yellowhammer nest success (White 2009, White *et al.* 2014). Lethal reduction of known nest predators of Ring-necked Pheasant using legal means had been carried out for some years at one site and not at all at two others, and the effects on breeding parameters such as nest success (separately for egg and chick stages of the nest cycle) had been estimated (described in White 2009).

Density-dependent effects will depend on specific circumstances. To investigate the impact of the form of the re-nesting probability function on population change, we used an equation of discrete population growth rate λ using parameters for the Yellowhammer population:

$$\lambda = p + l_\alpha b \qquad (1)$$

where $p$ is the adult annual survival rate, $l_\alpha$ is the survival rate from fledging to age at first reproduction, and $b$ is the number of female chicks fledged per female per season.

Yellowhammer demographic parameters entered into the model are given in Table 1. For $p$, we took the mean of adult survival rates associated with

**Table 1.** Parameters used to compare the predicted population consequences of different seasonal productivity models for Yellowhammer for a scenario where no predators were removed versus with predator removal (see text).

| | | | | Model included in... | |
|---|---|---|---|---|---|
| Parameter | Scenario | Value | Units | Deterministic | Individual-based |
| Daily survival egg stage $DSP_E$ | No predator removal | 2.876 ± 0.121 | logits | X | X |
| | Predator removal | 4.386 ± 0.273 | logits | X | X |
| Daily survival chick stage $DSP_N$ | | 2.920 ± 0.138 | logits | X | X |
| Chicks per successful nest $\Phi$ | | 2.76 | chicks | X | |
| Mean no. of attempts $\eta$ | | 2.52 | attempts | X | |
| Clutch size | | 1.233 ± 0.050 | ln(eggs) | | X |
| Proportion of eggs laid that hatch | | 1.599 ± 0.113 | logits | | X |
| Proportion of chicks hatched that fledge | | 1.575 ± 0.151 | logits | | X |
| Re-nesting function | Empirical | See Figure 1b | probability | | X |
| | Low step | See Figure 1b | probability | | X |
| | High step | See Figure 1b | probability | | X |
| First-year survival $l_\alpha$ | | 0.481 | probability | X | X |
| Adult survival $p$ | | 0.503 | probability | X | X |

Predator removal had an impact on daily survival probability at the egg stage but not at the chick stage. All other parameters were the same for each scenario. The re-nesting model was run for three different re-nesting probability functions (see Fig. 1b). Overall, four seasonal productivity models were run: a deterministic model, and the individual-based model specified once with each of the three re-nesting probability functions. The population model was then run for each predator removal scenario, making eight runs in total.

declining and increasing population trends for Yellowhammer populations (Siriwardena & Robinson 2002). For $l_\alpha$ we also took the mean for first-year survival for declining and increasing populations of Yellowhammer, but we then multiplied this by an estimate of post-fledging survival (i.e. survival from fledging to independence). Empirical estimates of post-fledging survival for British farmland passerines are few – we only found explicit estimates for Song Thrush *Turdus philomelos* of 0.798 over 14 days (Robinson *et al.* 2004). For populations of six Nearctic species, post-fledging survival ranged from 0.29 to 0.75 (Anders & Marshall 2005), for Starling *Sturnus vulgaris* in North America from 0.39 to 0.62 (Krementz *et al.* 1989), and for an urban Blackbird *Turdus merula* population, it was 0.57 (Magrath 1991). As a compromise, we took the mean value of these estimates, 0.51, which was congruous with the 0.45–0.55 range simulated by Bradbury *et al.* (2000) for declining and pre-decline Yellowhammer populations.

The number of female chicks fledged per female per season $b$ was taken from two types of seasonal productivity models: (1) a simple deterministic model that effectively took the product of a mean number of attempts made, a mean number of chicks per successful nest, and estimates of nest success, and (2) the individual-based model, parameterized with each of the three possible re-nesting probability functions (Fig. 1b). In both cases we assumed a 1:1 sex-ratio of chicks (Pagliani *et al.* 1999).

For the deterministic model we adapted a model from Paradis *et al.* (2000):

$$b = 0.5\Phi\eta\,(\mathrm{DSP}_E)^E(\mathrm{DSP}_N)^N \tag{2}$$

where $\Phi$ is the chicks fledged per successful nest, $\eta$ is the mean number of nesting attempts per female per season, $E$ is the typical egg period of a nest that survives from the first egg to hatching, inclusive of laying (days), $N$ is the typical nestling period of a nest that survives from hatching to fledging (days), and $\mathrm{DSP}_E$ and $\mathrm{DSP}_N$ are daily survival probability estimates from those periods, respectively.

For the three individual-based models specified with each re-nesting probability function, we took the main output from the models, mean fledglings per female per season, and halved it so it would represent mean fledglings per adult per season, assuming a 1:1 sex ratio in the breeding population given the species is monogamous (Sundberg 1994). The predator removal study had found a significant positive effect of predator removal on Yellowhammer $\mathrm{DSP}_E$ but no significant effect on $\mathrm{DSP}_N$ (Table 1). Overall mean nest success (taken as $(\mathrm{DSP}_E)^E(\mathrm{DSP}_N)^N$ from Equation 2) was predicted as 22% when predators were not removed, and 43% when predators were removed, a 95% relative increase (White 2009). We therefore calculated eight values of chicks fledged per female per season by running each of the four model types (deterministic, and IB parameterized with each of the three different $\varphi_R$ functions in Fig. 1b) for each of the two values of $DSP_E$ (with predator removal, without predator removal). These were then used to estimate $\lambda$ via Equation 1. Estimates of $\lambda$ represent the potential for population growth in the absence of density-dependent effects. We then compared how the use of each type or specification of seasonal productivity model influenced the predicted population-level effect of predator removal on Yellowhammers.

## RESULTS

For clarity, sections are lettered (A, B, C) to match the Methods section and their place in the framework in Figure 1.

### [A] Using pattern-oriented modelling to assess the re-nesting model

Comparing across a range of reproductive patterns, POM revealed a relatively close match between observed and simulated populations (Table 2, Fig. 3). The simulations tended to underestimate the number of attempts and the season productivity (compared for Black Redstart only), the latter by 0.4–0.8 fledglings per female per season. Simulations also had slightly lower measures of between-female variation (as measured by sd values) in number of attempts and seasonal productivity but still showed substantial variation in expected populations. A pattern seen across the POM assessment was that mean or sd values from simulations using the empirical $\varphi_R$ function tended to be intermediate between those of the high step and low step $\varphi_R$ functions, as was the case in almost every value (mean or sd) compared.

When comparing distributions of initial first-egg dates between observed and simulated populations (Fig. 3), for Black Redstart there was a good visual match between the simulation and observed data using both the empirical and low step $\varphi_R$ functions, showing a stepped pattern of decreasing frequency from initiations of first, to second, to third attempts, and each distribution looking approximately normally distributed (at least for first and second attempts). The Kolmogorov–Smirnoff tests indicated that these two simulated distributions

**Table 2.** Pattern-oriented modelling table for comparing observed and simulated Black Redstart and Yellowhammer breeding seasons using an individual-based model.

| | | | | Simulated with re-nesting function | | |
|---|---|---|---|---|---|---|
| Species | Pattern | | Observed | Empirical | High step | Low step |
| Black Redstart | Clutch initiation period (day) | Mean | 60.7 | 62.9 | 55.3 | 65.2 |
| | | sd | 0.7 | 0.3 | 0.4 | 0.4 |
| | Number of attempts | Mean | 1.68 | 1.56 | 1.58 | 1.47 |
| | | sd | 0.64 | 0.54 | 0.50 | 0.55 |
| | Relative frequency of number of attempts (%) ± multinomial se | 1 | 41.6 ± 3.3 | 46.6 | 42.6 | 55.6 |
| | | 2 | 49.1 ± 3.3 | 51.2 | 57.0 | 41.5 |
| | | 3 | 9.3 ± 1.9 | 2.2 | 0.4 | 2.9 |
| | Seasonal productivity | Mean | 6.0 | 5.5 | 5.6 | 5.2 |
| | | sd | 3.5 | 2.7 | 2.5 | 2.8 |
| | | Range | 0–16 | 0–15 | 0–10 | 0–15 |
| Yellowhammer | Clutch initiation period (days) | Mean | 58.1 | 61.8 | 50.1 | 73.6 |
| | | sd | 2.0 | 0.4 | 0.3 | 0.6 |

Black Redstart data are from a marked, intensively studied population (Weggler 2006) so accurate attempt and seasonal productivity data are available, alongside frequency of initiations over time per attempt, whereas Yellowhammer data are from an unmarked population so only distribution of nest initiations (attempt number unknown) over time is available. Clutch initiation time represents timespan between 10th and 90th centiles of clutch initiation dates. Note clutch initiation period mean and standard deviations (sd) are from 10 000 bootstrap samples with replacement, whereas for seasonal productivity and number of attempts they are from the original 10 000 runs. Samples sizes are: 226 observed Black Redstart female-seasons, 732 observed Yellowhammer nesting attempts, or 10 000 simulated female-seasons. se, standard error.

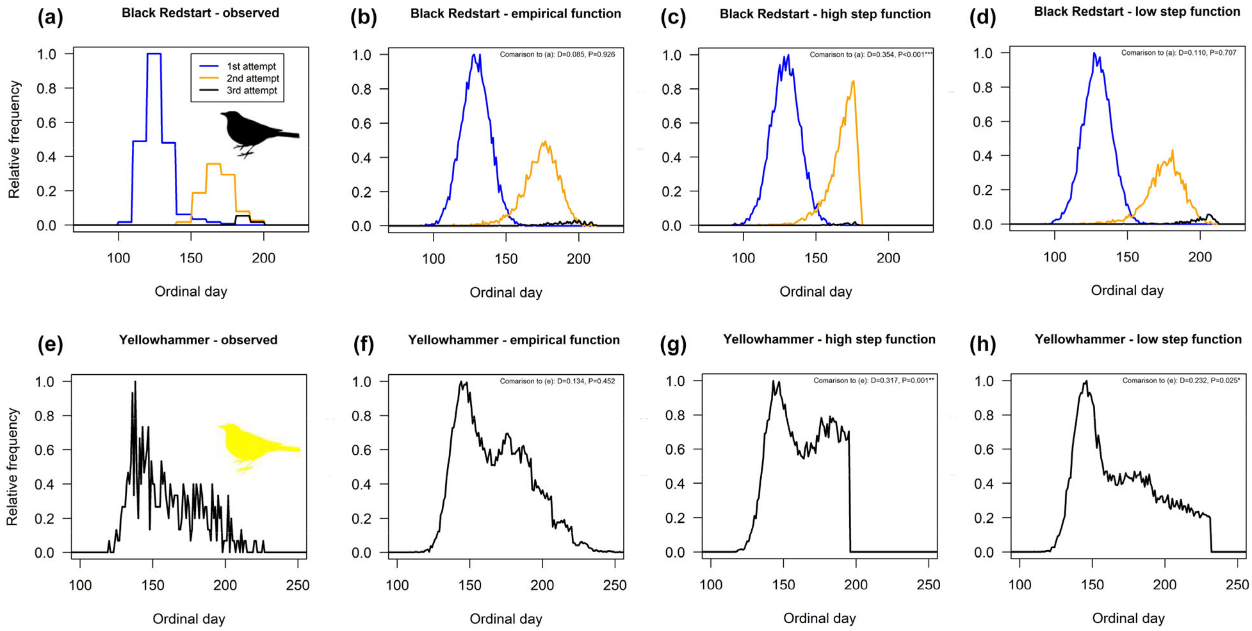

**Figure 3.** Pattern-oriented modelling comparison between observed (first column) and simulated distributions of initial first-egg dates for Black Redstart (top row) and Yellowhammer (bottom row). Simulations differ only by the re-nesting probability function used (see Fig. 1). For Black Redstart we knew the identity of each attempt (first, second or third) so these are separated by colour, but for Yellowhammer this was not known so they are combined. All simulations are from 10 000 female-seasons whereas observed samples sizes are: Black Restart 226 female-seasons, Yellowhammer 732 nesting attempts. *D* and *P* respectively refer to the test statistic and *P* value of Kolmogorov–Smirnov tests of that particular simulated distribution against the observed distribution (note the part of the distribution compared was only from the peak to where the observed population reached zero attempts, thus avoiding inflated similarity – see main text).

were not significantly different to the observed distribution (Kolmogorov–Smirnoff statistics displayed on plots). For the high step function, in contrast, the distribution of initiations of second attempts (and third attempts although this is less clear owing to low sample size) had a higher peak (i.e. more second attempts initiated) but was then clearly truncated at the point where the re-nesting probability changed from 1 to 0 (compare with Fig. 2a), meaning that the pattern looked very different to that of the observed population. This was reflected in the Kolmogorov–Smirnoff test result indicating a significant difference to the observed distribution.

Although the Yellowhammer initial first-egg distribution data were not separated by attempt, as with the Black Redstarts, the similarity in distributions of the observed and simulated populations appeared better for simulations using the empirical and low step $\varphi_R$ functions, in having a large initial peak and then a decay in initiations as the season progressed. There were some apparent differences between the distributions; for example, the simulation with the empirical $\varphi_R$ function showed a clearer second peak which probably partially represents a wave of initiations of second attempts, which was not as apparent in the observed data or low step simulation. Nevertheless, the Kolmogorov–Smirnoff test showed that the simulation with the empirical $\varphi_R$ function was the only simulation to not significantly differ in terms of initial first-egg distribution from the observed data. As with Black Redstart, for Yellowhammer the high step function resulted in a sudden cessation of nest initiations at a time in the season when these continued in the real population. Concurring with the apparent better visual match in first-egg date distributions for simulations with the empirical $\varphi_R$ function, clutch initiation period (a measure of season length that removes the effect of outliers) was most similar to the observed data for both species, relative to the high step and low step functions, which tended to underestimate and overestimate season length respectively (Table 2).

## [B] How does the re-nesting probability function influence re-nesting compensation?

The emergent property of re-nesting compensation behaved differently between $\varphi_R$ functions in both species. The predicted negative relationship between nest success and number of attempts differed between functions for both Black Redstarts (Fig. 4a) and Yellowhammers (Fig. 4b). In each case the relationship was weakest for the low step function. In Black Redstarts the relationship was strongest for the high step function and intermediate for the observed function (Fig. 4a), whereas in Yellowhammers (Fig. 4b) the high step and empirical functions showed similar strength relationships. At high levels of nest success, a similar number of attempts per female was simulated regardless of function used, but at lower values of nest success, the number of attempts predicted from models depended more strongly on the $\varphi_R$ function used.

## [C] What is the knock-on effect in a population model?

For the scenario where Yellowhammer nest success increased from 0.22 to 0.43 (a 95% increase) in response to predator control, as observed in White (2009), there were clear differences between predictions of the deterministic productivity model and the individual-based model (Fig. 5). Because the deterministic model does not modify the estimate of attempts made in response to variation in nest success (i.e. it does not simulate re-nesting compensation), there is a commensurate 97% increase in seasonal productivity per female. In consequence the predicted relative increase (41%) in population growth rate is larger than in the individual-based models (23–29%, depending on $\varphi_R$ function), where re-nesting compensation is an emergent property and 'dampens' variation in nest success by modifying the number of attempts. The resultant dampened change in seasonal productivity leads to lower estimated relative changes in population growth. Furthermore, within the individual-based model, the selection of different $\varphi_R$ functions, which influences the extent to which the model simulated re-nesting compensation (Fig. 4), in turn influences the modification in number of attempts made, the dampening effect this has on change in seasonal productivity, and ultimately the resultant estimate of relative change in population growth rate. The empirical $\varphi_R$ function gave an intermediate population growth increase estimate (26%) between the low step (29%) and high step (23%) functions.

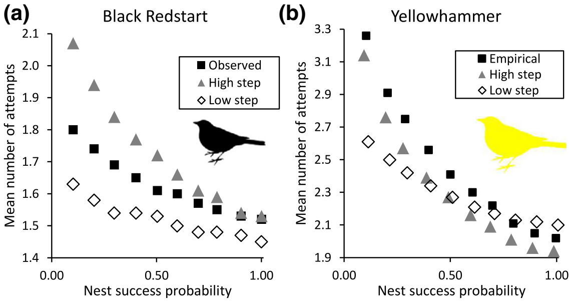

**Figure 4.** Relationship between nest success and number of attempts made in an individual-based model for (a) Black Redstarts and (b) Yellowhammers when parameterized with observed/empirical, high step and low step re-nesting probability functions (see Fig. 1).

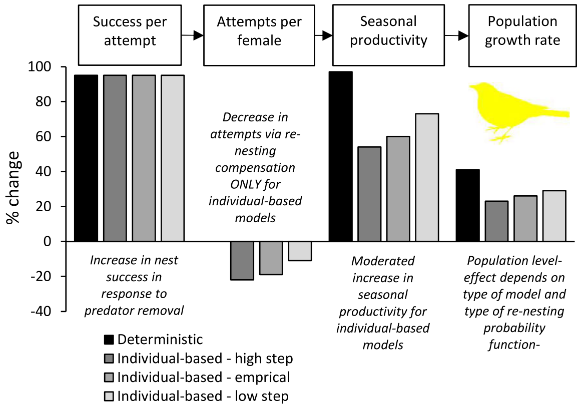

**Figure 5.** The predicted population growth consequences of a 95% relative increase in nest success in Yellowhammer (from 22% to 43%) as seen in response to predator control during a study in England, for an individual-based seasonal productivity model (parameterized with three re-nesting probability functions, see key and Fig. 1b) versus a deterministic seasonal productivity model. The plot should be read from left to right. Because in the deterministic model the number of attempts is fixed, seasonal productivity increases proportionately to nest success, and predicted population growth rate increases substantially. In the individual-based model, however, regardless of the $\varphi_R$ function used, the increased nest success leads to fewer attempts (due to re-nesting compensation, see Fig. 4b), and thus reduced increases in both seasonal productivity and predicted change in population growth rate. Values in this plot are given in the Supporting Information Online, Appendix S5.

## DISCUSSION

### What do individual-based re-nesting models offer?

Deterministic models of seasonal productivity miss two important processes seen or predicted in natural breeding populations: (1) that there is wide variation in the number of attempts made per female (e.g. Weggler 2006), and (2) that nest success and number of attempts are not independent of each other in space and time, meaning re-nesting compensation may occur (Nagy & Holmes 2004). Individual-based re-nesting models address these constraints by allowing the number of attempts made per simulated female not to be a fixed parameter, but rather an emergent effect of (ideally) empirical probability distributions, which determine (1) when each female starts breeding, (2) how long each attempt lasts and (3) when each female quits breeding. We demonstrated this by showing that our individual-based re-nesting model generated realistic between-female variation in number of attempts made, and realistic phenology of those attempts (as demonstrated via pattern-oriented modelling and comparison to a marked and intensively studied population; analysis A), which allowed the model to simulate re-nesting compensation (analysis B), a process that then 'dampened' the predicted increase in seasonal productivity and hence the population-level impact of a predator removal management intervention via a reduction in the mean number of attempts made (analysis C).

In contrast to the individual-based model, the deterministic model could not account for re-nesting compensation as it used a fixed estimate of number of attempts, and so produced a higher estimated impact of the management intervention (predator removal) on seasonal productivity and resultant predicted population growth rate. In theory, one could try to account for re-nesting compensation in deterministic models by adjusting number of attempts as well as data on the success of each attempt, but the problem remains that the mean number of attempts made is rarely known (see Cornulier *et al.* 2009), nor is the precise relationship between nest success and number of attempts. The benefit of an individual-based stochastic re-nesting model is that number of attempts (and variation in attempts between females) is an emergent effect of the model. Because re-nesting compensation has not been studied extensively (to our knowledge), comparisons of this relationship to real populations are limited. However, the observed pattern of re-nesting compensation for both species, of a non-linear negative slope with gradient decreasing with increasing nest success, closely matched that seen in a re-nesting model by Flint *et al.* (1998) for a population of Northern Pintails *Anas acuta*, which is the only such plot of nesting success versus number of attempts that we know to be in the literature.

There are areas where the individual-based re-nesting model could potentially be improved. For example, the modelling process was simplified by assuming that all successful attempts have an equal likelihood of contributing to the next generation. However, temporal variability in both the output of successful attempts, and subsequent recruitment from these, is likely. In Yellowhammer, for example, clutch size (Parkhurst & Lack 1946) and nest success (Barkow 2005) can vary across the season, and in other passerines there is evidence that later fledged chicks have lower post-fledging survival (Krementz *et al.* 1989) and lower recruitment into the breeding population (Mallord *et al.* 2008). This aspect could be coded into the model, for example by specifying distributions of breeding parameters according to time in season, or giving productivity outputs as a function of date, rather than as a final value per female. Powell *et al.* (1999) suggest that models that do not include a measure of female survival during the breeding season may overestimate productivity, and this could be accounted for as well (although see discussion in Supporting Online Information Appendix S2 on re-nesting probability functions). Our model assumed that every female was subject to the same probability functions with respect to breeding parameters, but number of attempts made and numbers of young fledged can be influenced by adult age (Weggler 2006, Hatch & Westneat 2007); future models could be run for age-classes of birds parameterized separately from empirical observations, and then a weighted average taken of outputs. As Beintema and Muskens (1987) noted, re-nesting may be influenced by external factors other than date, and this could be explored.

Some of these assumptions and simplifications might explain why the individual-based re-nesting models did not perfectly replicate patterns seen in the observed populations. For example, for Black Redstart, seasonal productivity and the number of attempts (and variation in these values) were slightly lower in the simulations than the real data, and fewer females had third attempts (c. 2%) than in the real population (c. 9%). It could be that within the Black Redstart population, there were processes or population structures not captured in the input parameters we used, such as temporal variation in breeding output per attempt or inter-attempt intervals, or else age/stage-based variation in breeding output. Weggler (2006) did find that 1-year-old females had significantly fewer attempts than 2- or 3-year-olds; such a pattern could be captured by incorporating age-based $\varphi_R$ functions but we did not have those available. The individual-based model we developed is open-source and could be adapted to consider such temporal or stage-based processes or patterns where empirical data are available to parameterize them. We do not think, however, that these differences modify the key finding of this study, which is that choice of seasonal productivity model (deterministic versus individual-based) and, for the latter, specification of re-nesting probability function, influences whether re-nesting compensation occurs and its strength. This, in turn, has implications for population-level predictions, as well as influencing the extent of between-female variation in breeding parameters.

## Does the shape of the re-nesting probability function matter?

We demonstrated here that individual seasonal-productivity models of the type used in earlier studies (e.g. Pease & Grzybowski 1995, Powell *et al.* 1999) can produce relatively accurate estimates of seasonal productivity, as well as simulate important internal patterns and processes, such as the distribution of attempts in a season and re-nesting compensation. But a second important investigation was the extent to which the re-nesting probability function itself, which determines the distribution of when females quit the breeding season, influenced model behaviour and output. Previous models had used simplified step functions that appeared biologically unrealistic. That is not to say that such simplifications were wrong (and in such cases an empirical re-nesting function was not available) nor gave inaccurate results. For example, Grzybowski and Pease (2005) showed that a high step parameterization produced accurate productivity estimates compared with observed data. Rather, using a biologically more realistic function might not only improve accuracy but also modify how models behave with respect to variation between females and to population-level consequences of variation in nest success. Comparing three models each specified with a different re-nesting function (two simplified functions and the observed function), a clear result was that simulations specified with the empirical $\varphi_R$ function tended to produce key output parameters and distributions that were intermediate between those of high step and low step functions and, in the case of distribution of initial first-egg dates and duration of breeding season (as measured by clutch initiation period), were closer to those of the observed population.

As re-nesting compensation works through failed females' ability to re-nest, whereas successful females are still 'investing' time in an active attempt, it follows that the parameter that drives the probability of re-nesting would influence this process. Consistently across both species, the weakest relationship between nest success probability and mean number of attempts in our trials came when the model was specified with the low step function. This makes sense in that the low step function has a lower probability of re-nesting in the first half of the season, and the first half of the season contains proportionally more attempts. Hence, there is less chance of simulated females re-nesting following early failures when this function is used. The reverse of this effect holds for the high step function, which specifies that in the first half of the season an early-failing female will always re-nest. This generated predicted population consequences for Yellowhammer, but not of great apparent magnitude, with impact on growth rate of predator control (relative to no predator removal) varying only between 23% with the high step function and 29% with the low step function.

As a result, we cannot say for certain that the shape of the re-nesting function matters definitively and in all cases when running an individual-based seasonal productivity model, particularly if the objective is simply to obtain some kind of single estimate of mean seasonal productivity. However, if future iterations of such a model include parameters that vary across the season (as discussed above), it may matter more, and we find that varying the re-nesting probability function does vary model outputs, particularly the degree of variation (as measured by sd) between females. Thus, trying a range of re-nesting probability functions for an individual-based productivity model may broaden a model's functionality. In addition, it could be that variation in this function is included in sensitivity analyses of future models (i.e. researchers see how sensitive their model outputs of interest are to this function), or that model outputs themselves are used to calibrate the optimal function for a given study population (Rykiel 1996). The comparison with simple step functions was carried out because such functions may be all that is available to researchers wanting to use individual-based seasonal productivity models for their study population.

### How to obtain a biologically more realistic re-nesting function

If researchers wish to use a range of re-nesting probability functions, there needs to be a way to obtain these. As Beintema and Muskens (1987) predicted for species that commonly lay replacement clutches, a re-nesting function must be close to 1 at the beginning of the season and then decline, but more research was needed to quantify its shape. We demonstrate here two ways whereby researchers may arrive at a more biologically realistic re-nesting function. The first, using data from an intensively studied marked population of Black Redstarts, is likely to be challenging since few such datasets seem to be available. The second involves a novel method of using incomplete nest records of unmarked populations, coupled with information on the proximity of temporally separate attempts that have a high likelihood of being from the same female (Supporting Online Information, Appendix S1). Although this approach makes several assumptions (discussed in more detail in the Supporting Online Information, Appendix S2), it produced a reverse-sigmoid shape broadly similar to that directly observed in Black Redstarts, and simulated a closer match of the distribution of first-egg dates to the observed population than simpler step functions. Newton (1999) and Newton and Rothery (2005) observed via adult post-breeding moult in Eurasian Bullfinches and European Greenfinches *Chloris chloris* that the dates of final nesting attempts were approximately normally distributed in most years. A reverse-sigmoid can represent the inverse of a cumulative (± skewed) normal distribution, so concurs with this.

Other indirect means of approximating a re-nesting probability exist. For example, Newton and Rothery (2005) examined the relationship between breeding and morphological characteristics such as extent of post-breeding moult and presence of a brood patch in European Greenfinches (their data are reproduced with permission in Supporting Online Information, Appendix S7). As the post-breeding moult begins during or shortly after the final breeding attempt, and as the female brood patch regresses after incubation of the final attempt, such information may serve as a proxy for a re-nesting probability function, or at least to estimate its approximate shape. The approach is not perfect, because Newton and Rothery (2005) found considerable overlap between moult onset and the final breeding attempt.

## CONCLUSIONS

Despite many advances, modelling of seasonal productivity is still a developing field (Cornulier *et al.* 2009, Etterson *et al.* 2011). Useful and adaptable dynamic models have been built that have the functionality for variable re-nesting functions to determine quitting dates (e.g. Pease & Grzybowski 1995, Mattsson & Cooper 2007) but simplified step functions have been used in the absence of empirical data on function shape. Here we show that where empirically based functions are available, which more closely match a real re-nesting probability distribution, they modify the outputs and behaviour of such models. We also present a novel method for estimating the shape of such functions in populations of unmarked birds. Being less resource-intensive than the monitoring of marked individual birds through a whole season, this may make estimating such functions easier for researchers. Other potential indirect methods involve the observation of female post-breeding moult or brood patch presence. Alternatively, researchers implementing dynamic seasonal productivity models could try a range of reverse-sigmoid-type functions (potentially drawn from data on moult or brood patches) and select the best fitting curve via model calibration. Importantly, regardless of how they are derived, we have shown that time-variable re-nesting functions can widen the functionality of seasonal productivity models in terms of specification of inter-female variation in breeding parameters and simulation of re-nesting compensation. Our demographic predictions demonstrate that, when investigating population-level consequences of drivers that impact nest success, the choice of model matters. Individual-based models that simulate re-nesting compensation make substantial changes to population growth predictions, which may influence our understanding of drivers of declines in multi-brooded bird species, or the probable impact of conservation interventions to assist them.

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## AUTHOR CONTRIBUTIONS

**Patrick J. C. White:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Chris Stoate:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; visualization; writing – original draft; writing – review and editing. **Nicholas J. Aebischer:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **John Szczur:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Lucy Ferrer:** Data curation; project administration; validation. **Ken Norris:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing.

## CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest related to this study.

## ETHICAL NOTE

None.

## FUNDING

None.

## Data Availability Statement

The individual-based re-nesting model, pre-populated for Black Redstart and Yellowhammer examples, is available at https://github.com/pjcwhite/individual_based_renesting_model. It includes instructions for set up and how to freely access NetLogo. An example view of part of the Netlogo interface is shown in Supporting Online Information, Appendix S6. Further information is available within the model when opened in NetLogo. R code and example data for aspects of the study that used R are also in this repository.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Derivation of different re-nesting probability $\varphi_R$ functions for Yellowhammers.

**Appendix S2.** Practical considerations regarding the adapted capture–recapture method in Appendix S1.

**Appendix S3.** Input parameters used in the base individual-based models for Black Redstart and Yellowhammer.

**Appendix S4.** Assessing whether 10 000 is sufficient model runs to achieve stable and precise model outputs.

**Appendix S5.** More detail on the population-level predictions.

**Appendix S6.** Example NetLogo outputs.

**Appendix S7.** Examples of other possible data sources for estimating re-nesting probability functions.