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Nest timing, nest site selection and nest structure in a high latitude population of Bearded Reedlings *Panurus biarmicus*

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ABSTRACT

Capsule: Bearded Reedlings *Panurus biarmicus* show consistent nest timing, select old, compacted areas of reed when positioning their nests, and may adjust nest structure in relation to local reed characteristics and temperature.

Aims: To investigate the nest timing, nest site selection and nest structure of a rare and elusive passerine, the Bearded Reedling at the northern limit of this species' range.

Methods: A sample of Bearded Reedling nests from the Tay Reedbeds in Scotland were located and monitored with regard to the timing of nesting, fate, fine-scale habitat characteristics and nest structure.

Results: First egg dates and brood sizes were consistent between years of the study despite variation in spring temperatures. Bearded Reedlings nested within unmanaged patches of reed, positively selecting deep leaf litters and compacted reed. Attributes of nest structure, namely internal and external diameter, were influenced by nest site characteristics and local temperature.

Conclusion: Despite a limited sample size, the study suggests that reedbed management should ensure adequate areas of old, dry and unmanaged reed are available when aiming to encourage breeding Bearded Reedlings. Additionally, the apparently flexible structure of the nest may assist this species when coping with changeable climatic conditions.

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Nesting is a vital stage in the annual cycle of a bird, being clearly linked to individual fitness and thus having consequences for the wider population (Streby *et al.* 2014). Understanding the nesting decisions of birds, and the processes influencing these decisions, is fundamental when developing successful strategies for species conservation. In rare or highly specialist species, nesting information is often sparse as fewer nests are available for monitoring. As specialist species are often the most vulnerable to habitat modification or climatic change (McKinney 1997, Colles *et al.* 2009), studies which focus on collecting nesting information in these species are likely to provide relevant insight for conservation.

The Bearded Reedling *Panurus biarmicus* is an open cup nesting passerine highly specialized to *Phragmites australis* reedbeds. Information concerning the nesting habits of this species is limited in comparison to other, more generalist, species due to the Bearded Reedling's strict specialization to reedbed habitats. Reedbeds are normally managed by harvesting or altering water levels in order to impede vegetative succession and preserve the long-term integrity of the reedbed (Hawke & Jose 1996, Poulin *et al.* 2002, Valkama *et al.* 2008).

Commonly, reedbed management has the additional motive to provide high-quality habitat for breeding birds (Hawke & Jose 1996, Gilbert *et al.* 2005). Understanding nesting decisions of reed specialist birds such as the Bearded Reedling could, therefore, directly enhance these management regimes. Further, while the wide range of the Bearded Reedling has led to its categorization as 'of least concern' on the IUCN's red list (BirdLife International 2014), it is a specially protected species in the UK (Eaton *et al.* 2009) and can undergo wide population fluctuations (Wilson & Peach 2006), the causes of which may be associated with nesting.

Breeding birds must decide the timing of nesting, the selection of a nest site and the structure of the nest itself. By understanding flexibility in the timing of breeding, predictions can be made about the potential implications of climatic change. Nest timing decisions must take account of both food abundance and climatic conditions. In many species, photoperiod regulates physical preparations for breeding (Visser *et al.* 2010), however, yearly variation in egg laying dates (Spitzer 1972, Both & Visser 2005), suggests that other, less rigid, external factors may also influence nest timing (Potti 2009, Visser *et al.* 2009, Thorley &

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Lord 2015). A nest-box study at Leighton Moss, England, suggests that Bearded Reedlings initiate breeding in mid-March (Wilson 2005). This species can then have several broods throughout the summer, into August (Cramp & Perrins 1993). Surmacki & Stępniewski (2007) provide evidence of variation in the first egg dates of Bearded Reedlings, with birds laying earlier in years with high spring temperatures. In multi-brooded species this flexibility may be important in allowing earlier breeding times and consequentially the production of more broods.

Understanding the nest site selection processes of bird species can offer further insight for conservation. Local scale management can seek to provide the most preferred characteristics of nesting habitat. These may be characteristics that assist the avoidance of predation, with birds known to select components of the habitat that minimize encounters with predators (Lima 2009). Nest site selection should also optimize microclimatic conditions. For example, Lesser Black-backed Gull *Larus fuscus* chicks in areas sheltered from prevailing winds have shown faster growth rates (Kim & Monaghan 2005). Additionally, stochastic events, such as flooding (Robertson & Olsen 2015) should be considered when selecting nest sites.

Several studies have used population level surveys to study the breeding distribution of the Bearded Reedling and infer important habitat components (Báldi & Kisbenedek 1999, Poulin *et al.* 2000, 2002, Beemster *et al.* 2010). These indicate that the species is limited to reedbeds and positions its nests within old stands of reed. However, fine-scale nest site selection is still poorly understood in this species, with most studies remaining unquantified (Wawrzyniak & Sohns 1986, Van den Elzen 1993). One study in Austria (Hoi & Hoi 2001) suggests that nests are positioned in wet, dense reed. Variation in structure between reedbeds and differences in management regimes, mean that studies from separate reedbeds may highlight important between-site differences with further relevance to management.

Finally, the structure of the nest itself may play a significant role in the success of a breeding attempt. As separate species show distinct nest structures well suited to providing sufficient support for the developing offspring, nest design was traditionally considered the product of stereotyped, inflexible behaviour (Wallace 1867). More recently, however, intraspecific and time-dependent variation in nest structure suggests flexibility in nest construction, which may be linked to climatic conditions (Mainwaring *et al.* 2012, 2014a), predator avoidance (Lima 2009, Biancucci & Martin 2010, Prokop & Trnka 2011, Marasco & Spencer 2015) or experience (Walsh *et al.* 2010, Muth & Healy 2011). In such species,

if altering nest design increases breeding success, this plasticity may be a means to buffer against the consequences of climatic variation.

Local information on Bearded Reedling nest structure exists for some populations within continental Europe (Wawrzyniak & Sohns 1986, Van den Elzen 1993), but information remains limited from populations in the UK. As this species is limited only to reedbed habitats, nest structure is relatively unusual (Wawrzyniak & Sohns 1986), with further information from local sites potentially offering insight into how this species copes with climatic variation over its extensive range. For example, higher latitude populations, exposed to colder temperatures might be expected to increase the insulating properties of their nests (Hansell 2000).

This study seeks to investigate the timing, nest site selection and nest structure of Bearded Reedlings to better establish the relationship between this species and its specialized habitat. We study one of the most northerly breeding populations in Europe, at the Tay Reedbeds in Scotland. As this population is at the edge of the Bearded Reedling's geographic range, it offers a useful system in which to study nesting decisions towards the climatic limits that this species can tolerate. Additionally, this site is managed in the form of winter reed cutting to provide heterogeneity in the reed structure for breeding birds. Thus, information on fine-scale nesting decisions can be directly incorporated into future management. In this study, we monitored a sample of nests and report the timing of first broods. We then quantified the local nest site characteristics in order to better determine fine-scale nest site selection. Finally, we report measurements of nest dimensions and relate these to local nest site characteristics and climate to identify those factors influencing variation in the nest structure of this species.

Methods

Study site

The study was undertaken at the Tay Reedbeds, Scotland (56°23.00'N, 3°10.00'W) in spring 2013, 2014 and 2015. This is the largest continuous stand of common reed on the British Isles, extending for around 4.1 km². The stretch of the reed in which the nests were located varied in width (distance from the land edge to the river edge), between 200 and 450 m. While the vast majority of the reedbed consisted of dense, uninterrupted stands of reed, in each year small patches of reed were harvested in the winter. These cut patches remained clear of vegetation between January and March, before they were re-occupied by new reed

growth which began in April and reached maturity by July. Our study area constituted both areas with large stands of uncut reed, and areas which included a mosaic of cut patches.

Nest location and monitoring

We located nests in the early breeding season (April and May), as they became more difficult to find later in the season due to dense new growth reducing the access to the reedbed (Wawrzyniak & Sohns 1986). Adult Bearded Reedlings captured for ringing were examined for the presence of a brood patch in females or a cloacal protuberance in males (following Svensson 1992). When birds were caught in breeding condition a point transect extending the length of the reedbed was undertaken. This involved visiting vantage points at raised locations along the land edge boundary of the reedbed and provided a general indication to where breeding activity was occurring. Areas of high activity were subsequently visited and potential nest sites identified by watching birds consistently returning to the same areas. These areas were searched and the nest position recorded using a handheld global positioning system device. The population was also the subject of an ongoing habitat selection study, which meant that several of the nests located belonged to either colour-ringed or radio-tagged adults, allowing identification of individual breeding birds.

Upon locating a nest, a record was taken of the finding date, clutch size and age of the chicks. First egg dates were retrospectively calculated by subtracting, from the finding date, the age of the chicks, 12 days for incubation (Cramp & Perrins 1993) and an additional number of days equal to the brood size of the given nest. When nests were located at the egg stage, effort was made to record the hatching date, from which first egg date could be estimated. Nests were visited minimally: on initial location, when verifying hatching dates on nests located at the egg stage, and when ringing the chicks. The fate of the nest was recorded as successful if it fledged any young and unsuccessful if it was predated or failed for other reasons such as starvation in the nest. Empty nests that had successfully fledged were distinguishable from predated nests as adults feeding fledged young were often conspicuous around the nesting area at the predicted fledging dates.

The initial point transect covered the full reedbed, meaning breeding activity was recorded in a range of sites within this reedbed. Further, as nests were located over a range of reed characteristics, these factors are unlikely to have caused bias in detectability.

Quantifying nest site characteristics

After the nest became inactive, the reed characteristics of the nest site were quantified. The height of the nest above the ground was measured to the nearest cm. The mean height of five old, dead reed stems within 1 m from the nest indicated old reed height. The mean number of dead stems touching a 1 m long stick, inserted horizontally at a height of 1 m from the ground in 5 evenly spaced directions around the nest allowed quantification of old stem density. These methods were also used to measure the height and density of new, live, reed stems after the initiation of new growth. However, when new growth was below 1 m in height, the stick was inserted at half of the height of the new stems.

Areas of old dense reed that had begun to lean over were given a rating of 1 to 5, with 5 being the most compacted areas. This rating was termed the degree of reed stagger (here on referred to as 'stagger'). Mean leaf litter depth in three directions around the nest was also measured to the nearest 5 cm. Finally, the mean percentage of water cover around the nest to the nearest 10% was calculated from 3 measurements taken using a 0.5×0.5 m quadrat within a 3 m radius from the nest.

In order to compare nest sites with unoccupied sites, reed characteristics were also measured at random locations that were unoccupied by breeding Bearded Reedlings. The study site consisted of a mosaic of reed types: reed cut in the previous winter, young reed which had been left uncut for between 1 and 5 growing seasons and old, previously uncut reed. Despite searching in all patches of the mosaic, every nest was located in old, previously uncut reed (see results). Thus, the choice of random, unoccupied, locations was limited to areas of this old reed. This allowed a comparison of local reed characteristics between occupied and unoccupied sites of old reed, and inference of the key reed characteristics considered in nest site selection within this reed type. Sixteen random locations were generated in QGIS (QGIS Development Team 2012) but constrained to be more than 10 m from a real nest location. The number of random locations equalled the number of nests located. Measurements at an unoccupied site were taken within a week of measurements taken at a real nest.

Quantifying nest dimensions

Nests were collected and frozen for a minimum of two weeks and no longer than four weeks, before being dried at room temperature for a further two weeks. After this, six nest characteristics were measured following Mainwaring *et al.* (2014a) (Figure 1). The external diameter of the nest was measured as the mean of the outer diameter at the widest and narrowest axes. The internal diameter was the mean of

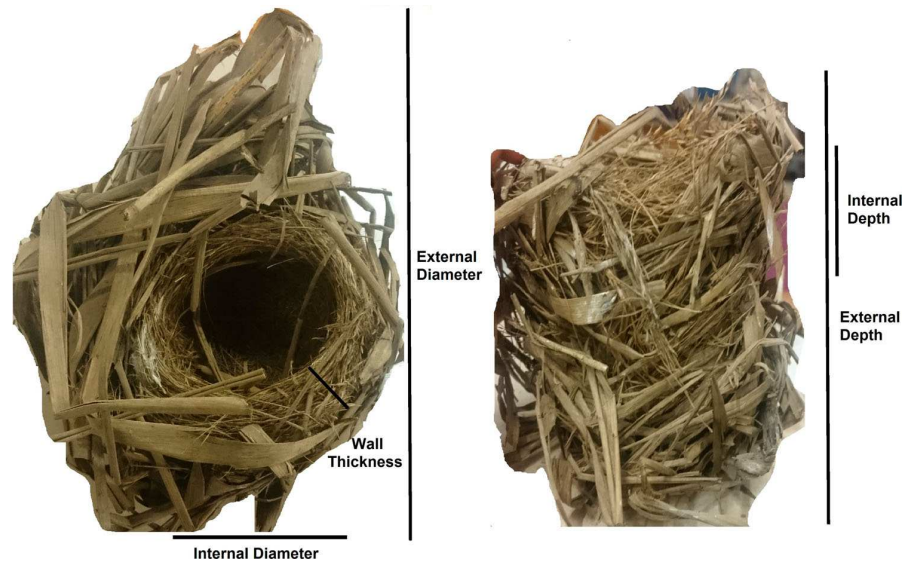


Figure 1. A single Bearded Reedling nest collected from the Tay Reedbeds and recorded nest dimensions. Left panel shows the top of the nest, while the right panel is the view from the side.

the internal cup diameter at the widest and thinnest axes. The external nest depth was the distance from the top of the nest to its external base. The internal depth was the distance from the top of the nest to the lowest point in the cup. Wall thickness was measured by inserting a pin through the wall at half of the internal cup depth, then taking the average of four measures at evenly spaced intervals. All nest measurements were recorded to the nearest 1 mm. Finally, nests were also weighed (grams to the nearest 0.1 g) using digital scales. Only an external examination was used to qualitatively describe component materials. On completion, the nests were added to Glasgow University's nest archive (Russell *et al.* 2013).

Analysis

The first egg dates, mean brood sizes and number of nests surviving were calculated for each year and are presented with the mean spring (March–May) temperatures in eastern Scotland for each year (Met Office UK, 2015). Additionally, having exact locations of the nests allowed the distances from the land and river edges of the reedbed to be calculated. The distance from the nearest cut patch was also calculated for nests within 500 m of a cut patch. Distances were not included in any of the nest site selection models as sample sizes prevented subsetting of data between managed and unmanaged sites. Similarly, while we obtained too few nests to model the factors influencing nest predation, we provide details of individual nest fates in online Supplementary Material 1.

All data analyses were conducted in R version 3.1.1 (R Development Core Team 2011). Reed characteristics that could predict the probability of a site being occupied by a Bearded Reedling nest were identified using a logistic modelling approach. This involved assigning a binary response to the local nest site data, indicating whether the measurements were taken at an occupied nest site or an unoccupied random location. This binary response was then modelled in a logistic regression with each of the reed characteristics as explanatory variables.

To avoid collinearity in the explanatory variables, prior to modelling, Pearson's correlation coefficients were calculated for each pair of covariates. We avoided the use of principal component analyses due to its potential instability when conducted on datasets with low sample sizes (Guadagnoli & Velicer 1988). Instead, when variables were highly correlated (Pearson's correlation was significant to an alpha level of 0.01), we included only a single variable from the correlated pair in the full model. From each correlated pair, we retained the variable which contributed most to nest site selection. The most parsimonious logistic model was selected using a backwards stepwise selection procedure based on the Akaike information criterion (AIC) values of each model. The goodness of fit of the logistic model was tested using the Hosmer and Lemeshow goodness of fit test (Hosmer & Lemeshow 2000) in R package *ResourceSelection* (Lele *et al.* 2014).

We investigated how the dimensions of the nests themselves were related to local nest site characteristics and climatic variables. We first tested how different

structural aspects of the nests were associated with each other using Pearson's correlations. We then tested whether these variables could be predicted by the reed characteristics at their given nest site using linear models (LM). Due to small sample sizes, explanatory variables were used to explore each nest attribute individually.

Each nest was assigned a temperature based on the mean minimum temperature experienced during nest building. This was estimated as the mean daily minimum temperature (data provided by www.wunderground.com, 2015, *Ilogfor10* station within 5.5 km from the reedbeds, 0 m above sea level) during the five days prior to first egg date. Here on, this is referred to as the 'building temperature'. Bibby (1983) notes that Bearded Reedlings can continue assembling the nest into the chick stage, and so nest dimensions may more closely correlate with the mean minimum temperature over the period during which the nest was active. Thus, LM were also run with the mean daily minimum temperature from the first egg date to the last date the nest was seen active. This is subsequently referred to as 'after-laying temperature'. Mean minimum temperature was used, rather than overall mean temperature, in order to emphasize the variation in the most extreme cold conditions that birds were subject to.

Results

Nest timing

In total 16 Bearded Reedling nests were located. Eight were initially located at the egg stage and eight at the nestling stage. Almost all were found within the main fieldwork period between 5 April and 14 May. One nest was located outside this period, with its first egg date on 21 June 2013. Table 1 details the overall first egg dates and brood sizes in each year. No nests were located at the building stage or during the laying period and so full incubation times were not recorded. Two nests that were located when they contained eggs subsequently fledged successfully, allowing an accurate observation of the time spent in the nest as chicks. This was for 11 and 12 days, respectively. Additionally, two of the nests were second broods of birds for which the first nests had been located. In these two cases, the

Table 1. Summary of breeding parameters in the three years of study for Bearded Reedlings in the Tay reedbeds.

Year	Number of nests located	First egg date	Mean clutch size (min, max)	% Nests successful	Mean spring temperature (°C)
2013	3	13 Apr	6.7 (5,7)	100	6
2014	7	5 Apr	5.8 (5,7)	57	9
2015	6	5 Apr	5.0 (5, 5)	16	7.7

birds had laid the first egg of their subsequent brood five and six days after their first brood was predated.

Of the 16 nests, 8 (50%) fledged at least one young. This was variable between years (Table 1). Nest failure was caused by predation at the chick stage in 4 (50%) of the unsuccessful nests. Only one nest (13%) failed at the egg stage; due to egg predation. The remaining 3 (37%) unsuccessful nests were in 2015 when chicks were found dead in the nest at variable ages. Online Supplementary Material 1 provides the reed characteristics and nest fates for individual nests.

Nest site selection

All nests were located in mature stands of reed that had not previously been cut. Nests were a mean distance of 180 m (± 16.8 se) from the land edge and 109 m (± 13.2 se) from the river edge. Twelve (75%) nests were within 500 m of a cut patch, with the mean distance of these from the nearest cut edge being 29.8 m (± 4.9 se). Table 2 summarizes the reed characteristics recorded around the nest sites and random, unoccupied sites.

Of the habitat characteristics, old reed density and degree of stagger showed a significant positive correlation (Pearson's $r = 0.65$, $P < 0.01$), as did the height and density of new reed stems (Pearson's $r = 0.79$, $P < 0.01$). From these pairs of covariates the degree of stagger and density of new stems contributed most to the selection model and were retained. Thus, the full logistic regression model included the height of old reed, degree of stagger, the density of new reed stems, leaf litter depth and the percentage of water cover around the nest. This model suggested that occupied sites had higher stagger ratings and leaf litter depths than unoccupied sites (Table 3; Figure 2).

Nest dimensions

Nest dimensions were recorded for 15 of the nests; 1 was excluded due to damage sustained from a predation event and subsequent rain prior to its collection. All of the nests were exclusively constructed from *Phragmites*, with different features of the reed being used to build

Table 2. Summary of reed characteristics recorded at occupied Bearded Reedling nests sites and at unoccupied random sites.

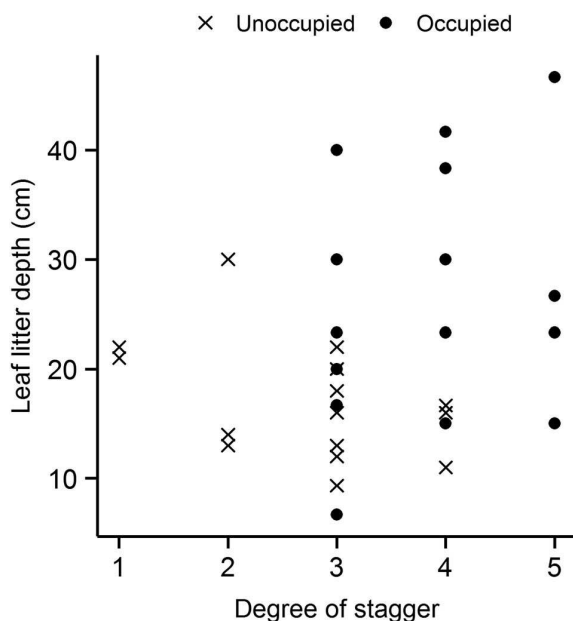
Reed characteristic	Mean (se)	
	Occupied	Unoccupied
Old height (cm)	282.3 (5.4)	254.2 (5.55)
Old density (stems)	26.8 (1.0)	22.1 (1.1)
Degree of stagger	3.9 (0.2)	2.7 (0.2)
New height (cm)	61.0 (15.3)	59.3 (17.8)
New density (stems)	9.8 (1.7)	9.2 (1.4)
Leaf litter (cm)	26.6 (2.8)	16.9 (1.3)
Water cover (%)	5.0 (2.0)	11.5 (2.7)

Table 3. Summary of logistic regression models comparing occupied Bearded Reedling nest sites against unoccupied random sites.

Covariate	Δ AIC	Estimate (se)	P
Degree of stagger	0	1.71 (0.81)	0.03
Leaf litter (cm)	0	0.16 (0.08)	0.04
Water cover (%)	0	-0.09 (0.05)	0.15
Old height (cm)	1.38	0.03 (0.03)	0.23
New density (stems)	1.58	-0.08 (0.09)	0.5

different layers of the nest (Figure 1). *Phragmites* leaves formed the main bulk of the structure, being woven to form a thick cone-shaped base. Broken *Phragmites* stems of differing sizes provided the main structure for the cup which was thickly lined with soft *Phragmites* seed panicles. This pattern of construction was common to all of the nests located, with all three components being present and occupying the same function in each nest. No nests included additional components, such as other vegetation.

However, the size and quantity of the components differed between nests, resulting in considerable variation in the nest dimensions (Table 4). Nests with large external depths tended to have large internal depths (Pearson's $r = 0.59$, $P = 0.026$). The deepest nests were also the heaviest (Internal depth: Pearson's $r = 0.71$, $P = 0.003$; External depth: Pearson's $r = 0.57$; $P = 0.023$). There was a slight negative relationship between

**Figure 2.** Leaf litter depths and the degree of reed stagger from raw data in occupied Bearded Reedling nest sites and unoccupied patches of mature reed. Residual deviance of most supported model: 22.8 on 28 degrees of freedom; Hosmer and Lemeshow Chi-Squared₅ = 8.2, $P = 0.15$.**Table 4.** Dimensions of features of 15 Bearded Reedling nests collected from the Tay reedbed.

Nest Dimension	Mean (se)	Min	Max
Height above ground (cm)	32.8 (4.21)	6	69
External diameter (cm)	12.2 (0.14)	9.0	14.5
Internal diameter (cm)	6.0 (0.21)	4.7	8
External depth (cm)	9.7 (0.71)	6.3	16.1
Internal depth (cm)	5.0 (0.19)	3.2	6.1
Wall thickness (cm)	1.9 (0.12)	1.0	2.8
Weight (g)	29.7 (4.1)	14.8	61.4

the thickness of the wall and internal nest diameter but this was not significant (Pearson's $r = -0.43$, $P = 0.11$). There was no relationship between the brood size in the nest and the internal depth (Pearson's $r = 0.01$, $P = 0.94$), internal diameter (Pearson's $r = -0.28$, $P = 0.31$) or any other nest dimensions.

Nests located in areas of high reed density and stagger showed dense, deep cone-shaped bases. This was because nests in these areas were often built into tight gaps within the staggered reeds, becoming misshapen and requiring thick, compacted external depths to remain stable (LM: external depth and density of old stems $F_{1, 13} = 19.55$, $P < 0.001$; LM: external depth and stagger $F_{1, 13} = 8.42$, $P = 0.012$). The internal depth showed a similar relationship to the density of old reeds ($F_{1, 13} = 8.15$, $P = 0.014$). Smaller nests (with a thinner external diameter) were located in areas with a higher density ($F_{1, 13} = 11.62$, $P = 0.005$) and height of new reed growth ($F_{1, 13} = 16.45$, $P = 0.001$).

Nests had larger external diameters if they were exposed to lower mean minimum temperatures both during building (LM: $F_{1, 13} = 8.81$, $P = 0.01$) and after laying (LM: $F_{1, 13} = 4.35$, $P = 0.05$; Figure 3). Wall thicknesses was unaffected by the mean minimum temperature during building (LM: $F_{1, 13} = 1.18$, $P = 0.20$). However, wall thickness (LM: $F_{1, 13} = 4.35$, $P = 0.05$) showed a negative relationship with the mean minimum temperature after laying (first egg date to last date seen active). One individual bird had two of its nests located, and another had three of its nests located during the study. These individuals showed distinct variation in external diameter of their located nests, with larger diameters when the building and after-laying temperatures were lower (Figure 3).

Discussion

This study provides new information on the Bearded Reedling in respect to the timing of breeding, the general features and specific character of the preferred nest site, the structure of the nest and the flexibility shown in nest construction. Despite a relatively small sample size these factors could have implications for

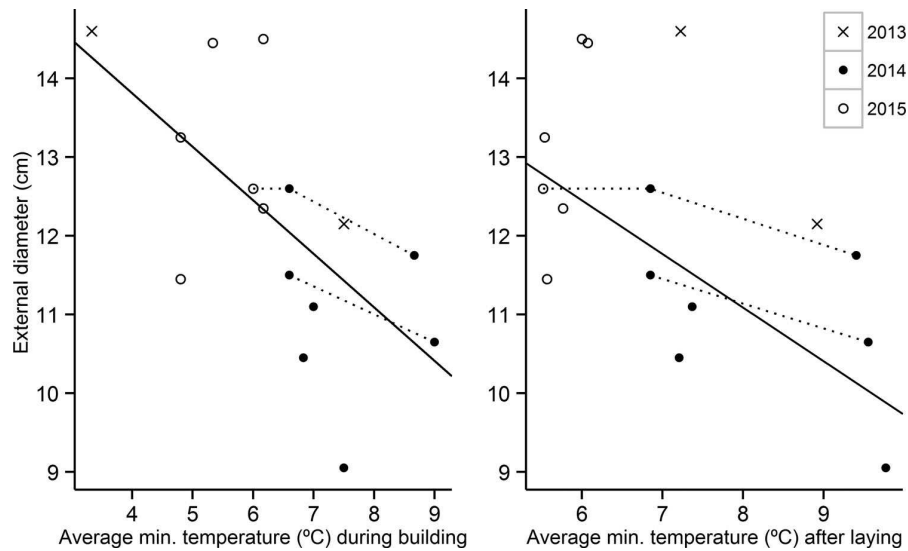


Figure 3. Size of the external diameter of Bearded Reedling nests from the Tay Reedbeds, and the average minimum temperature over the building period (period five days prior to first egg date) and after egg laying. Solid line represents the overall regression. Dotted lines are drawn between nests build by the same individual.

the management and conservation of this reed-dwelling specialist.

Bearded Reedlings on the Tay began nesting at the start of April. Lower latitude populations tend to begin breeding slightly earlier than this, with Wilson (2015) reporting that 30% of first egg dates in a long-term nest-box study at Leighton Moss reedbed in northern England, occurred in March (also see Bibby 1983, Cramp & Perrins 1993, Darolová *et al.* 2008). Beemster *et al.* (2010), demonstrate high peaks of fledged birds occurring in synchrony with the emergence of chironomids, which are a significant component of the diet of Bearded Reedlings (Bibby 1981, Beemster *et al.* 2010). Thus, synchronization with prey abundance looks to be an important component of nest timing decisions, and possibly drives the slightly later breeding times of higher latitude birds on the Tay. However, Bibby (1983) notes that earlier breeding times are apparent in eutrophic lakes, while tidal reedbeds are later, so it is unclear if these delays are related to the high latitude of this site.

Surmacki & Stepniewski (2007) show earlier first egg dates at higher spring temperatures in Poland. In our study, first egg dates remained consistent despite changes in spring weather conditions. Additionally, we saw rapid relaying times in individuals that had more than one nest monitored, suggesting a pressure to complete multiple breeding attempts in the available season. In multi-brooded species, earlier initiation allows more subsequent broods, causing a trade-off between beginning early and breeding at the most

optimal conditions (Crick *et al.* 1993, Kosinski 2001). For Bearded Reedlings, a high reproductive output may be a means to cope with the dramatic winter mortality experienced by this species (Wilson & Peach 2006). Longer term data on breeding phenology at the Tay, potentially available through ringing studies (Peach 2000), will better illuminate any trends related to climate in this population and further disentangle yearly and latitudinal variation in the timing of breeding.

All nests were located in old, previously uncut patches of the reedbed. It is unsurprising that reed cut the previous winter saw no nesting attempts, as the birds begin breeding before regrowth provides sufficient structure. In line with previous studies (Hoi 1989, Hoi & Hoi 2001, Beemster *et al.* 2010), we also found no nests in young reed that had remained uncut for between one and five growing seasons. Beemster *et al.* (2010), demonstrate that Bearded Reedlings show a preference for the oldest stands when nesting in a mosaic of old reed and young, previously grazed, reed. Additionally, Bearded Reedlings have been observed undertaking long foraging trips of around 500 m (Poulin *et al.* 2000, Beemster *et al.* 2010), suggesting nest site selection is not simply a function of proximity to feeding sites. Clearly, patches of old reed have an important role for nesting Bearded Reedlings.

The logistic models suggested that the highest chance of occupancy was in areas of old reed that had a high density of stems. Nests were also positioned in dense reed patches in lake Neusiedl, Austria (Hoi & Hoi 2001). Generally, predation rates of passerine nests

decline with stem density in reedbeds (Graveland 1997, Honza *et al.* 1998, Báldi & Batáry 2000, Poulin *et al.* 2002). Species such as Eurasian Reed Warblers *Acrocephalus scirpaceus* are even known to produce larger and heavier eggs when nesting in dense, more protected territories (Darolová *et al.* 2014). Additionally, our study also showed that the degree of reed compaction, or stagger, was positively selected during nesting decisions, with all nests occurring where there was a medium to high level of reed stagger. Few studies have considered the degree of reed compaction when investigating nest site selection or predation rates (although Tarr *et al.* 2004 conducted similar measurements). An artificial nest experiment conducted on the Tay reedbeds (Malzer & Helm 2015) highlighted the importance of this reed characteristic in reducing nest predation, potentially by increasing overhead cover and limiting avian predation. Wawrzyniak & Sohns (1986) also suggest overhead cover may function to reduce exposure to strong sunlight.

The selection for areas of high leaf litter, may, however, suggest additional factors are taken into account during nest site selection. Previous studies suggest leaf litter has little effect on nest predation in reedbeds (Batáry *et al.* 2004, Trnka & Prokop 2006, Schiegg *et al.* 2007, Malzer & Helm, 2015). A deep leaf litter in reedbeds can normally only develop in areas with infrequent inundation of water. Thus, this attribute may provide an indication to Bearded Reedlings that a given site is unlikely to flood. As most of the monitored nests were positioned near the ground, they may have been especially susceptible to inundation during high tide events at the Tay (also see Wilson 2005, Wilson & Peach 2006) and selection for dry areas that minimize this risk may be adaptive. Contrastingly, Hoi & Hoi (2001) report greater water depths in nesting areas used by Bearded Reedlings in the non-tidal Lake Neusiedl and suggest that the choice of these areas reduces predation from terrestrial predators. In tidal sites such as the Tay, inundation may be more frequent and less predictable, so causing birds to select safer, dry sites. This contrast in results suggests that nest site selection in this species varies between sites and may be dependent on site-specific pressures.

The nests located on the Tay showed similar dimensions to those reported for continental birds (Wawrzyniak & Sohns 1986, Van den Elzen 1993). For example, the external diameter for birds in the Czech Republic and Germany ranged from 8.0–12.0 cm to 7.5–17.0 cm, respectively, while Tay nests were 9.0–14.0 cm. Similarly, internal depth on the Tay ranged from 3.2 to 6.1 cm while nests from Austria and Germany ranged from 3.0–4.0 cm to 4.0–7.0 cm,

respectively. Our study suggested that the structure of Bearded Reedling nests on the Tay varied in relation to local nest site characteristics and temperature. As the density of old reeds and degree of stagger increased, nests were larger, with greater external and internal depths. This variation looked to be driven by the need to build a nest with a robust structure. Nests in sites with high stagger were built up against the reed and often compacted to fit within gaps, whereas nests in less dense areas were positioned directly in the leaf litter with shallow foundations. These results suggest Bearded Reedlings can alter their nests to suit local habitat structure, allowing them to exploit a variety of potential nest sites within old reed stands (Wawrzyniak & Sohns 1986).

The relationship of both external diameter and wall thickness with temperature, also suggested nest structure had a role in maintaining optimal microclimatic conditions. Several bird species have shown changes in the insulatory properties of their nests with decreasing temperatures (Hansell 2000, Crossman *et al.* 2011, Mainwaring *et al.* 2012, 2014a, 2014b). For example, Mainwaring *et al.* (2014a) showed that Blackbirds *Turdus merula* in cooler, more northerly parts of the British Isles had larger external diameters. We found, similarly, that Bearded Reedling nests exposed to lower temperatures when building had wider external diameters. Further, we saw thicker walls at higher temperatures when temperatures after laying were considered. The birds potentially construct larger nests when exposed to lower temperatures during building, and as temperatures change during the active nest stages, the wall size is altered. This is in line with previous studies which suggest alteration of the nest structure can continue into the active incubation and chick phases (Wawrzyniak & Sohns 1986). This effect was consistent in individuals that had several broods, suggesting that this flexibility is maintained between broods. The clarity in these results may be driven by the confinement of this species to few nesting materials, removing potentially confounding variation in the availability of nesting materials.

The conclusions of this study can be used to inform the future conservation management of reedbed habitats. Many reedbeds are subject to cutting, grazing or flooding management to reset succession and increase reed vigour. While these practices can provide effective foraging sites for reed specialists including the Bearded Reedling (Valkama *et al.* 2008, Beemster *et al.* 2010), our results clearly suggest that effective management should also ensure adequate areas of old reed are available as nesting habitat. As we found no nests in areas of reed uncut for less than five years,

when designating areas for nesting habitat, management should be excluded over the long term to allow adequate leaf litter and reed compaction to form. Indeed, where flexible hydrological control is possible, drawdown of water levels during the breeding season may provide further nesting habitat, offering drier areas of leaf litter. While this prescription may benefit the Bearded Reedling, management should also consider the requirements of other protected reedbed species. Eurasian Bitterns *Botaurus stellaris* require water depths of between 10 and 97 cm before nesting (Gilbert *et al.* 2005, Polak 2007), while Eurasian Reed Warblers may benefit from the presence of non-reed vegetation (Darolová *et al.* 2014). An effective strategy that is likely to offer resources for a range of species is that of a dynamic habitat mosaic where areas of old reed, early successional stages and open water can occur in parallel.

Our results also provide relevant information for the wider conservation of the Bearded Reedling. The ability of Bearded Reedlings to flexibly produce multiple broods could assist this species when coping with both inter-annual and long-term climatic variation. Similarly, being able to alter nest structure in relation to local temperatures may provide a means to buffer against environmental change. In understanding the factors governing fine-scale nesting decisions, conservationists can develop well-informed management strategies which may prove critical for the protection of rare and specialist species.

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