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RESEARCH ARTICLE

Experimentally quantifying the effect of nest-site depth on the predation risk and breeding success of Blue Tits

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ABSTRACT
Predation is a key factor in the nesting preferences of birds. Studies indicate that cavity-breeding birds prefer deeper nest sites, possibly because they are more safe from predation. We studied the Blue Tit (*Cyanistes caeruleus*), a cavity-breeding passerine, to test (1) whether nest-site depth affects breeding success and (2) whether potential effects of nest-site depth on breeding success are related to predation risk. We performed 2 experiments to separate effects of nest-box depth from potential effects of the quality of the breeding pair. In the first (free-choice) experiment, Blue Tits competed for scarce deep nest boxes that were provided well *before* nest-box choice, enabling an association between nest-box quality and bird quality. In the second (forced-choice) experiment, we randomly altered nest-box depth *after* Blue Tits had chosen a nest box, thus disconnecting the association between nest-box quality and bird quality. We found no evidence that the occurrence of signs of predation was related to nest-box depth. However, we did find clear positive effects of nest-box depth (1) on clutch size and hatching success throughout the study area and (2) on fledging success, the number of fledglings, and the overall probability of nest success, specifically in parts of the study area with high predation. We found no indication of independent effects of parental quality on breeding success. Parents also seemed to perceive the shallower boxes as more risky; in shallower boxes, nest thickness was decreased, irrespective of the local predation pressure during the free-choice experiment. Parents nesting in shallow boxes may have had lower breeding success because of (1) increased actual (but undetected) predation and (2) reduced reproductive investment by parents, based on the latter's experience with predation or an evolutionary response to past predation risk.

Keywords: animal behavior, cavity depth, competition, individual quality, perceived predation risk, predation danger, resource quality

Cuantificación experimental del efecto de la profundidad del sitio de anidación en el riesgo de depredación y el éxito reproductivo de *Cyanistes caeruleus*

RESUMEN
La depredación es un factor clave que determina las preferencias de anidación de las aves. Los estudios indican que las aves que anidan en cavidades prefieren sitios de anidación más profundos, potencialmente debido a que son más seguros ante la depredación. Estudiamos la especie *Cyanistes caeruleus*, un ave paserina que anida en huecos, para 1) evaluar si la profundidad del sitio de anidación afecta el éxito reproductivo y 2) evaluar si los efectos potenciales de la profundidad del sitio de anidación sobre el éxito reproductivo estuvieron relacionados al riesgo de depredación. Usamos un enfoque experimental para separar los efectos de la profundidad de la caja nido de los efectos potenciales de la 'calidad' de la pareja reproductiva. Realizamos dos experimentos: en el primer experimento, los individuos de *C. caeruleus* compitieron por unas pocas cajas nido profundas ofrecidas bastante *antes* de la elección de la caja nido (elección libre), permitiendo una asociación entre caja nido y 'calidad' del ave. En el segundo experimento, alteramos al azar la profundidad de la caja nido *después* que los individuos de *C. caeruleus* habían elegido una caja nido, desconectando la asociación entre caja nido y 'calidad' del ave (elección forzada). No encontramos evidencia que la ocurrencia de signos de depredación estuviera relacionada con la profundidad de la caja nido. Sin embargo, si encontramos claros efectos positivos de la profundidad de la caja nido sobre el tamaño de la nidada y el éxito de eclosión a través del área de estudio, y específicamente para sub-áreas con alta depredación, en el éxito de emplumamiento, el número de volantones y la probabilidad global de éxito de los nidos. No encontramos signos de efectos independientes de la calidad parental en el éxito reproductivo. Los progenitores también parecieron percibir a las cajas más superficiales como más riesgosas: en las cajas más superficiales el espesor del nido se redujo independientemente de la presión local de depredación durante el experimento de elección libre. Los progenitores

que anidaron en cajas superficiales pueden haber tenido un éxito reproductivo más bajo debido a 1) un aumento real, no detectado, de la depredación y 2) una reducción de la inversión reproductiva de los progenitores, basado en la propia experiencia frente a la depredación o basado en una respuesta evolutiva a un riesgo de depredación pasado.

Palabras clave: calidad del recurso, calidad individual, competencia, comportamiento animal, peligro de depredación, profundidad de la cavidad, riesgo percibido de depredación

INTRODUCTION

Key in the life of a bird is obtaining a safe site on which to raise its offspring. One important factor determining the suitability of a breeding site is the level of predation in the environment. Predation can affect fitness either directly, when predators target offspring and/or breeding parents, or indirectly through effects of perceived predation risk on parental investment (Lima 2009, Thomson et al. 2012, Hua et al. 2014, Ibáñez-Álamo et al. 2015).

As a consequence, breeding sites with lower predation risk are likely to be preferred (Møller 1988, 1989, Rauter et al. 2002, Lima 2009, Mainwaring et al. 2014; but see Chalfoun and Martin 2007, Chalfoun and Schmidt 2012). When scarce, this can lead to competition within and among species. More competitive individuals may claim the nest sites with lower predation risk, forcing the less competitive individuals to breed at sites with higher predation risk (Nilsson 1984, Candolin and Voigt 2001, Pärt 2001, Sergio et al. 2009, Thomson et al. 2012). In such a situation, it is challenging to disentangle which part of individual fitness is affected by traits of the individual and which part by the resources the individual is able to obtain (Sergio et al. 2009, Thomson et al. 2012, Germain and Arcese 2014). To disconnect the covariation between traits of breeding birds and their nest sites, researchers have (1) used statistical methods to explain the variation in breeding success with variables supposed to reflect the quality of the individual and/or the breeding site (Bart and Earnst 1999, Przybylo et al. 2001, Browne et al. 2007, Sergio et al. 2009, Germain and Arcese 2014, Zabala and Zuberogoitia 2014) and (2) used experimental approaches to eliminate potential effects of traits of the individual (Both and Visser 2000, Martin et al. 2000, Pärt 2001, Sirkia and Laaksonen 2009, Thomson et al. 2012).

In the present study, we used an experimental approach to separate the effects of traits of cavity-breeding Blue Tits (*Cyanistes caeruleus*) and of the nest site on breeding success. We focused specifically on one trait of the nest cavity, its depth. We tested (1) whether nest-site depth affects breeding success and (2) whether potential effects of nest-site depth on breeding success are related to predation risk. Previous work in our study population has shown that deeper nest boxes are preferred by Blue Tits and by their main competitor, the Great Tit (*Parus major*; R. W. Fokkema personal observation). This preference was previously shown in Great Tits, but not in Blue Tits, by

Löhrl (1977, 1986). One reason may be that deep nest boxes are safer from nest depredation by animals such as martens (*Martes* spp.), weasels (*Mustela nivalis*), woodpeckers (especially *Dendrocopos major*), and domestic cats (*Felis catus*; Wesołowski 2002, Czeszczewik and Walankiewicz 2003, Wesołowski and Rowiński 2012, Kaliński et al. 2014, Maziarz et al. 2016).

Nest-box depth could affect breeding success (1) directly through actual predation or (2) indirectly through adjusted parental investment in response to the "perceived" predation risk of broods in deeper and shallower nest boxes. How parents perceive predation risk in deeper and shallower nest sites is likely dependent on experiences within their lifetime (Lima 2009, Chalfoun and Martin 2010, Ibáñez-Álamo et al. 2015) but may also have evolved as a result of selection through predation in previous generations (Julliard et al. 1997, Sheriff et al. 2010). Results of previous studies indicate that both Great and Blue tit parents indeed seem to perceive shallower nest sites as more risky; parents decreased the thickness of the nest in shallower nest boxes, possibly in an attempt to reduce predation risk (Mazgajski and Rykowska 2008, Kaliński et al. 2014). In doing so, parents may face a trade-off between the potential fitness loss due to nest predation and the potential fitness loss due to the reduced thermoregulatory capacity of a thinner nest (Heenan 2013, Kaliński et al. 2014, Mainwaring et al. 2014). In response to higher perceived predation pressure in shallower nest sites, parents could—besides adjusting the thickness of the nest—also adjust their reproductive investment (e.g., clutch size, incubation effort, offspring feeding effort). It may be beneficial for parents in riskier, shallower nesting sites to reduce their reproductive investment, in order to be able to produce a repeat clutch in case of nest loss (Slagsvold 1982, 1984, Martin 1995, Farnsworth and Simons 2001).

Breeding success in shallower nest sites may thus be lower because of actual and/or perceived predation risk. However, parents breeding in deeper vs. shallower nest sites may also differ in their traits (see Fokkema et al. 2016), and this could affect breeding success independently from nest-site depth (Bart and Earnst 1999, Przybylo et al. 2001, Browne et al. 2007, Sergio et al. 2009, Germain and Arcese 2014, Zabala and Zuberogoitia 2014). Several studies indicate that parents may even differ in their behavioral response to predation, influencing their own and their offspring's predation risk (Lima and Dill 1990,
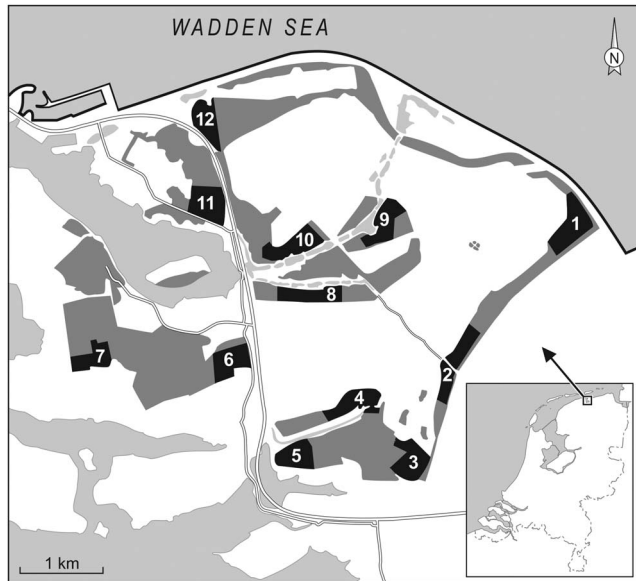
FIGURE 1. Map of the study plots located in the Lauwersmeer area, in the north of the Netherlands. The Wadden Sea and the Lauwersmeer Lake are depicted in light gray, the forest areas in dark gray, and the study plots in black.

Ghalambor and Martin 1999, van Oers et al. 2004, Nicolaus et al. 2012, Abbey-Lee et al. 2016).

To separately quantify the effects of parental traits and nest-box depth on predation risk and breeding success of Blue Tits, we performed 2 experiments. In the first (free-choice) experiment, Blue Tits competed for scarce deep nest boxes provided well *before* nest-box choice, enabling an association between nest box and bird quality. In the second (forced-choice) experiment, we randomly altered nest-box depth *after* Blue Tits had chosen a nest box, thus disconnecting the association between nest-box quality and bird quality.

Our expectations followed the framework specified by Sergio et al. (2009). (1) If neither nest-box depth nor parental traits affect breeding success, we expected no effects in either the free-choice or the forced-choice experiment. (2) If nest-box depth alone determines breeding success, we expected similar effects in both experiments. (3) If both nest-box depth and parental quality determine breeding success, we expected effects in both experiments, but stronger effects in the free-choice than in the forced-choice experiment. And (4) if only parental quality affects breeding success, we expected effects in the free-choice experiment only.

METHODS

Study Area and Study Species

The study took place in 2011–2014 in a Great Tit and Blue Tit nest-box population in the Lauwersmeer area in the north of the Netherlands (53.39°N, 6.24°E). The study area consisted of 12 study plots of 50 nest boxes each (Figure 1). Nest boxes were equally spaced every 50 m. The land area was reclaimed from the sea in 1969 and planted with mixed deciduous forest. The inside dimensions of all the wooden nest boxes in the area were ~12 cm in length, ~8 cm in width, and ~24 cm in height. The entrance diameter was 32 mm and located in the front panel ~16 cm from the base (measured from the inside of the box). A metal plate was fitted around the entrance for protection from predators such as woodpeckers and mammals that peck or chew open the nest hole (~10 cm in length, ~11 cm in width). These metal plates were left on the boxes during our experiments for practical reasons, which may have prevented predation from occurring in the above-mentioned way. The wooden plates from which the boxes were constructed were ~2 cm thick. The roof plate overlapped the sides of the box by ~3 cm.

Our study on the effect of nest-box depth on predation risk and breeding success was focused on Blue Tits. However, predation on Great Tit broods in our study area was monitored by using camera traps, in order to gain better insight on the type of nest predator active in our study area and its behavior (see below).

Standard Protocol

We conducted weekly nest-box checks of the whole study area to detect new tit nests during the breeding season and to monitor the breeding performance of those nests (see below). Using egg width (based on our population data), we determined the species (<12.4 mm: Blue Tit; >12.7 mm: Great Tit). Nests with intermediate egg width, inconclusive with respect to species determination (12.4–12.7 mm), were checked more frequently until we could determine the species when the tit was observed incubating the eggs. If a brood had fledged, we removed the nest material from the box and looked carefully through the material for any eggs or dead nestlings.

Nest-Box Depth Manipulations

We performed 2 experiments focused on the Blue Tits to measure the fitness consequences of nest-box depth separately from effects of traits of the breeding pair.

(1) Before nest building started (free-choice experiment). As part of a larger experiment (see Fokkema et al. 2016), in 2011 and 2012, well before the breeding season, we induced competition for deep nest boxes by drastically reducing nest-box depth in four-fifths of the available nest boxes. For each study plot of 50 boxes, we randomly assigned 10 nest boxes to stay deep; to reduce the depth of the remaining boxes, we added one 4.3 cm thick wooden block to 20 boxes and two 4.3 cm thick wooden blocks to the other 20. We thus created boxes with depths of 16 cm, 12 cm, and 7 cm, respectively (depth measured from the
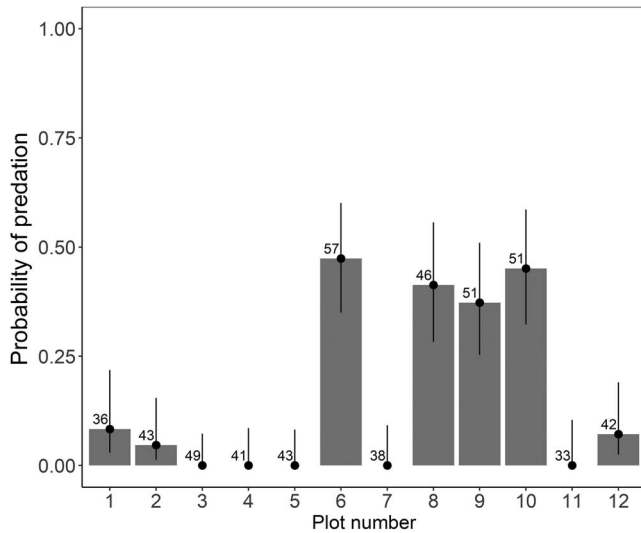
FIGURE 2. Probability of observing depredated Blue Tit broods per plot (used as a measure of predation risk) in our study area in the Netherlands. Predation was recognized by signs such as overturned nests, nests pulled through the entrance hole, and bitten-off remains of nestlings or adults outside or inside the nest box. Consistently over the study years, the predation risk of Blue Tit broods was higher in 4 study plots (predation plots) than in the rest of the study plots (non-predation plots). Sample size is indicated by the numbers next to the 95% confidence intervals.

lowest end of the entrance hole at the inside of the box to the bottom of the box; for further details, see Fokkema et al. 2016). Nest occupation was registered using the standard protocol (see above). Our expectation was that in this experiment, the distribution of birds over the deep and shallow boxes would depend on their competitive ability. The more competitive Blue Tits would get the deepest boxes, and the less competitive Blue Tits the shallow boxes. Note that we worked in a mixed nest-box population of ~170 Blue Tit breeding pairs and ~200 Great Tit breeding pairs. Blue Tits thus faced both intraspecific and interspecific competition. To separately quantify the effects of nest-box depth and of the breeding birds' traits on breeding success and predation risk, we needed to do an additional experiment.

(2) After egg laying started (forced-choice experiment). In 2013 and 2014, we altered nest-box depth, independent of the quality and choices of the breeding pair, after Blue Tits had started egg laying by placing either 1 or 2 wooden blocks underneath the nest. In 2013, as in the previous experiment in 2011−2012, blocks 4.3 cm thick were added. We noticed, however, that this did not work well for the treatment in which 2 blocks were added to the box; the nest was lifted too high and blocked the entrance in some cases. For 2013, we therefore stopped this treatment and used only nests to which either no or one wooden block was added in our analysis. In 2014, we

adapted the design and used blocks 3.3 cm thick; we were thereby able to get the full range of treatments (0–2 blocks).

If a new Blue Tit nest was found using the standard protocol (see above), we randomly assigned a treatment and altered the nest-box depth the following day (by repeating a sequence of 0, 1, or 2 blocks along the list of nests to manipulate that day). Such a treatment went as follows. First, the nest was loosened from the sides of the box by using a thin metal ruler. Next, the bottom of the box was taken out and either 1 or 2 wooden blocks were added underneath the nest. Nests under which no wooden blocks were added were also loosened from the sides of the box by using the thin metal ruler.

Nest-Box Depth and Predation Risk

In all 4 study years, we monitored nest depredation of Blue Tit broods in the nest boxes. All Blue Tit broods in the study area were checked on a weekly basis following the standard protocol (see above). In addition, Blue Tit broods were visited more often to measure nest thickness (see below) and, specifically within the forced-choice experiment, to measure the weight of the whole brood of Blue Tits when the nestlings were 5 days old (the latter measure is not analyzed here). In an opportunistic manner, we further noted any predation events (visible from signs of predation on the outside of the box; see below) observed when walking through the study area while on our way to visiting other Great or Blue tit broods in the area. On all these occasions, we registered a predation event (1) when a nest was pulled through the flight hole and/or turned over; and/or (2) when bitten-off remains of adults or juveniles were found on or near the nest box (in a vicinity of 2 m; following Wesołowski 2002, Misík and Paclík 2007, Kaliński et al. 2014).

Based on the above criteria, over the study years, we detected 93 predation events at 530 Blue Tit broods, 11 of which did not fail after predation (some offspring still fledged). It is important to note that here we focus on all predation that occurred after clutch initiation, because we could determine the species involved only when eggs had been laid (see above). We define predation risk here as the probability of detecting a predation event. Predation of Blue Tit broods consistently occurred in 4 of our 12 study plots (based on Figure 2; for study plots, see Figure 1). One reason for this spatial difference may be that the 4 study plots with higher predation were also the study areas with consistently higher densities of first broods (mainly broods of Great and Blue tits in our study area; density per hectare [± SE] for the predation plots: 3.69 ± 0.19; non-predation plots: 2.76 ± 0.11). This difference was significant (linear mixed-effects model with year and plot as a random factor to estimate the overall effect of plot type: $\chi^2 = 8.62$, df = 1, $P < 0.01$). Predators may have been more drawn to the

study plots with higher densities of breeding attempts. In our analyses of the effect of nest-box depth on breeding success, we took the spatial difference in predation risk into account (see below). In analyses of the effect of nest-box depth on the predation risk of Blue Tit broods, we focused on the 4 predation plots. To account for between-plot differences in breeding densities and the fact that the same plots were measured over different years (pseudo-replication), we included plot as a random factor in all analyses.

We used camera traps (Reconyx HC600 and Bushnell natureview HD) in 2012, 2013, and 2014 to identify the predator and learn more about its behavior. Over the years, camera traps were placed predominantly during the nestling-rearing phase (camera days in the nestling-rearing phase per year: 2012, $n = 37$; 2013, $n = 46$; 2014, $n = 137$). Data from camera traps were available for 22 broods (6 Blue Tit and 16 Great Tit broods) from the 4 predation plots (camera footage of predation on Great Tit broods was also taken into account here; see above).

Nest-Box Depth and Nest Thickness
We measured the thickness of all nests in both experiments. Potential nest-thickness adjustments by Blue Tits in response to nest-box depth could reflect how parents themselves perceive the predation risk in the deeper and shallower nest boxes (see above). In 2011 and 2012, we measured nest thickness on a random day in the period between the start of incubation and when the nestlings were 5 days old. In 2013 and 2014, nest thickness was measured at the end of the egg-laying period or during the incubation period. Nest thickness was measured on 2 places in the front rim of the nest using a knitting pin. The pin was inserted vertically left and right from the nest cup in the nesting material until it reached the bottom of the box. A light, 2 cm slider of iron wire was lowered along the knitting pin on the nest rim, its position fixed and the knitting pin including slider retracted from the nest. The average of the distance from the left and right measurements in centimeters between the slider (the surface of the nest) and point of the knitting pin (the bottom of the box) was taken as the nest thickness (adaptation of technique used by de Heij 2006).

Nest-Box Depth and Breeding Success
We measured 5 parameters of breeding success for the Blue Tit broods: (1) clutch size, (2) hatching success (the fraction of eggs from which a nestling hatched; for all nests in which incubation was initiated), (3) fledging success (the fraction of nestlings that fledged from the nest; for all nests that hatched ≥ 1 egg), (4) the number of fledglings produced (the number of nestlings that fledged from the clutch), and (5) the overall probability of nest success (in the period from clutch initiation until fledging).

Statistical Analyses
All data were analyzed using R 3.4.2 (R Core Team 2017). We used a linear mixed model with a Gaussian error structure to estimate the effect of nest-box depth on nest thickness. The effects of nest-box depth on the occurrence of signs of predation, hatching success, fledging success, and overall nest success of Blue Tit broods were all modeled with a generalized linear mixed model with a binomial error structure. The effect of nest-box depth on clutch size and the number of fledglings was tested with a generalized linear mixed model with a Poisson error structure. We used the package "lme4" (Bates et al. 2015) for our analyses. Post hoc analysis to test main effects of variables was done with the package "multcomp" (Hothorn et al. 2008), and significant interactions were tested using the package "lsmeans" (Lenth 2016). Figures were created using the package "ggplot2" (Wickham 2009), and the predicted lines in Figures 4, 5, 6, and 7 were created using the "predict" function.

Response variables and sample size. Our analysis of the effect of nest-box depth on overall nest success over the period from clutch initiation until fledging was based on all Blue Tit breeding attempts in which ≥ 1 egg was laid ($n = 530$). The effects of nest-box depth on clutch size, hatching success, and number of fledglings were analyzed for all broods in which birds had completed a clutch and initiated incubation ($n = 489$; in analyses of hatching success and number of fledglings, we included broods in which none of the eggs hatched). Fledging success was analyzed for those broods in which ≥ 1 nestling hatched ($n = 448$; we included broods in which no nestlings fledged). Hatching and fledging success were included as a construct of "successes" and "losses"; for hatching success, this was based on number hatched vs. number not hatched; for fledging success, it was based on number fledged vs. number not fledged (following Crawley 2007).

We analyzed the effect of nest-box depth on nest thickness for 482 Blue Tit broods for which nest thickness could be measured. To gain insight into the effect of nest-box depth on the predation risk of broods, we analyzed the effect of nest-box depth on the probability of a predation event (as defined above). For this analysis, we focused on 205 Blue Tit broods (predation plots only).

Predictor variables. We included nest-box depth as a continuous variable because we were interested in the direction of the effect of nest-box depth on the analyzed response variables. To evaluate whether results differed between our experiments, we included the interaction of study year and nest-box depth in all analyses (2011 or 2012 for free-choice experiment, 2013 or 2014 for forced-choice experiment). In our analyses of the effects of nest-box depth on nest thickness and parameters of breeding success, we included plot type (predation = 1, non-predation = 0; see above) and the interaction between nest-

FIGURE 3. A pine marten (*Martes martes*; the main predator in our study area in the Netherlands) attempting to depredate a Great Tit brood and the breeding parent early in the morning. In this attempt the marten was unsuccessful, but 2 days later it managed to depredate both the breeding parent and the brood.
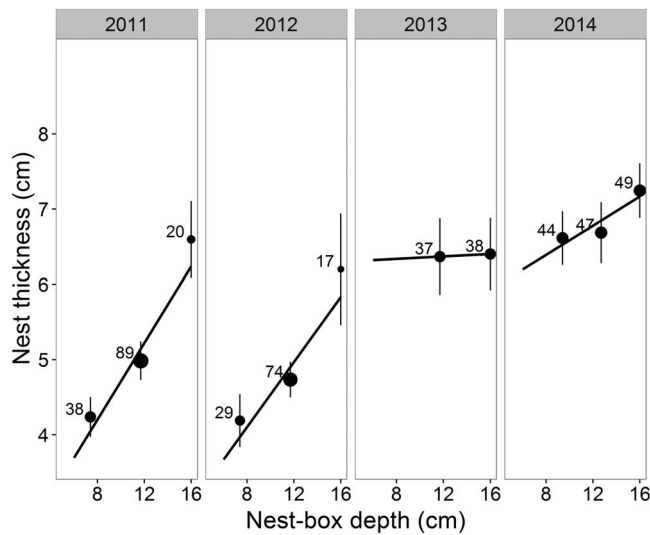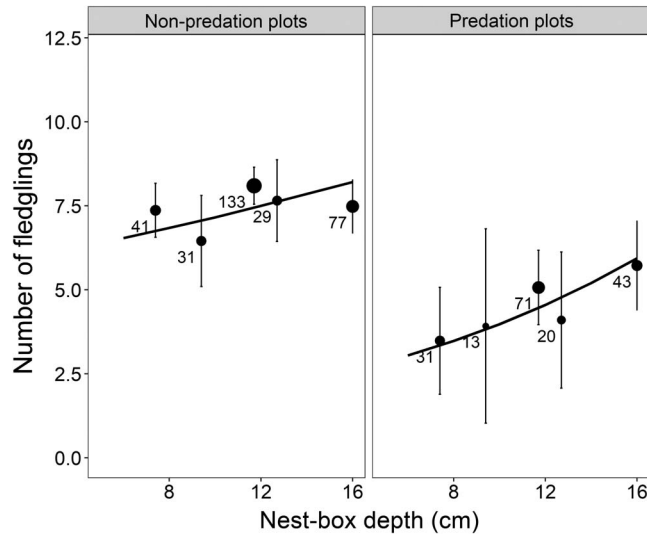

FIGURE 4. Effect of nest-box depth on thickness of Blue Tit nests in our study area in the Netherlands. The slope of the effect of nest-box depth differed significantly among study years. In the years in which nest-box depth was changed before the breeding season, Blue Tits reduced the thickness of their nests in shallower boxes (2011–2012). This effect was absent in the years in which we changed nest-box depth after clutch initiation (2013–2014). Sample size is indicated by symbol size and the numbers next to the 95% confidence intervals. Solid line depicts the predicted response calculated on the basis of the final selected model.
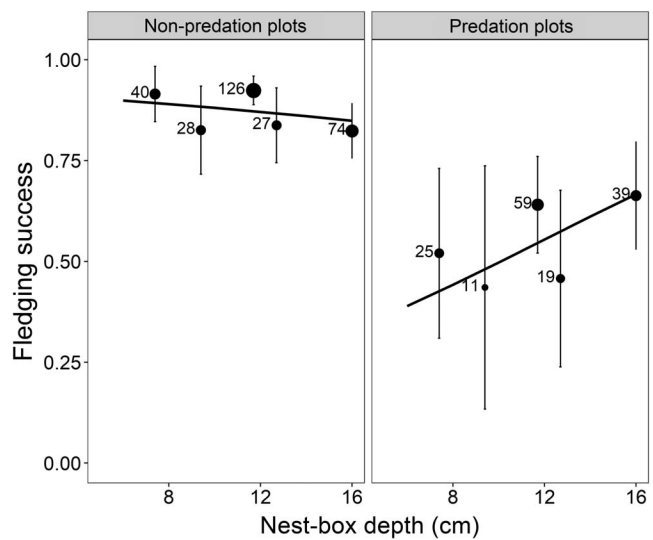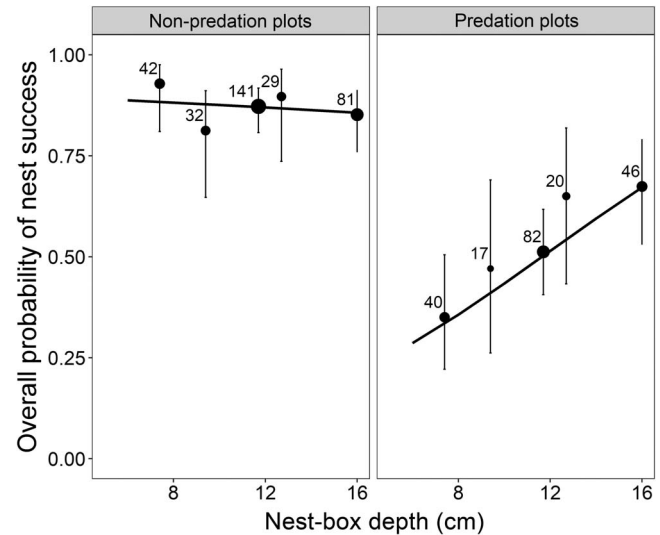

FIGURE 5. Effect of nest-box depth on fledging success of Blue Tits in our study area in the Netherlands. The slope of the effect of nest-box depth differed significantly between study plots with low predation risk (non-predation plots) and those with high predation risk (predation plots). Only in the predation plots did nest-box depth have a positive effect on fledging success. Sample size is indicated by symbol size and the numbers next to the 95% confidence intervals. Solid line depicts the predicted response calculated on the basis of the final selected model.

FIGURE 6. Effect of nest-box depth on Blue Tit fledgling number in our study area in the Netherlands. The slope of the effect of nest-box depth differed significantly between study plots with low predation risk (non-predation plots) and those with high predation risk (predation plots). Nest-box depth had a stronger positive effect on fledgling number in the predation plots than in the non-predation plots. Sample size is indicated by symbol size and the numbers next to the 95% confidence intervals. Solid line depicts the predicted response calculated on the basis of the final selected model.

FIGURE 7. Effect of nest-box depth on overall probability of nest success in Blue Tits over the period from clutch initiation until fledging in our study area in the Netherlands. The slope of the effect of nest-box depth differed significantly between study plots with low predation risk (non-predation plots) and those with high predation risk (predation plots). Only in the predation plots did the probability of nest success increase in the deeper boxes. Sample size is indicated by symbol size and the numbers next to the 95% confidence intervals. Solid line depicts the predicted response calculated on the basis of the final selected model.

box depth and plot type. In our analyses of hatching success and fledging success, we included clutch and brood size, respectively, as additional predictor variables to account for the fact that these variables, independently, could exert effects. We included study plot as a random factor in all our analyses (see above).

Predictor selection. We used a backwards elimination procedure to eliminate predictor variables that did not significantly reduce the deviance of the model based on likelihood ratio tests. We first tested whether the interactions between nest-box depth and all included predictor variables could be eliminated. We then proceeded by removing the predictor variables in order of their significance. The random effect of study plot was left in the model at all times because it was there to correct for pseudoreplication.

RESULTS

Predator Identification

On 10 different days, we detected a nest predator using the camera traps during the nestling-rearing phase of Great and Blue tit broods (2 days in 2012, 5 days in 2013, 3 days in 2014; see above). In all cases, the predator was a marten (*Martes* sp.). In at least 2 cases (including the one shown in Figure 3), the predator could be identified as a pine marten (*Martes martes*; see Supplemental Material Video S1).

Four of the recorded predation attempts in 2013 and 2 in 2014 were at the same brood on different days. Analysis of the images and video material, combined with data gathered by regular nest-box inspections, shows that only in 5 of the 10 cases that a marten was recorded at a nest on a camera did it successfully depredate nestlings or the breeding bird. Among the 5 occasions that we photographed or filmed a marten successfully depredating a brood and/or breeding bird, in only 2 cases did it actually leave signs. The dataset was too limited to test the effect of nest-box depth on the risk of marten predation.

Nest-Box Depth and the Predation Risk of Blue Tit Broods

Signs of predation. Within the predation plots, predation risk differed significantly between years (year: $\chi^2 = 44.13$, df $= 3$, $P < 0.001$). In 2012, 2013, and 2014, significantly more predation events were recorded than in 2011 (post hoc multiple comparison, 2012 vs. 2011: $\beta = 2.69 \pm 0.47$, $z = 5.78$, $P < 0.001$; 2013 vs. 2011: $\beta = 1.42 \pm 0.56$, $z = 5.78$, $P = 0.05$; 2014 vs. 2011: $\beta = 1.76 \pm 0.45$, $z = 3.94$, $P < 0.001$; 2013 vs. 2012: nonsignificant; 2014 vs. 2012: nonsignificant; 2014 vs. 2013: nonsignificant). Correcting for these year differences, we found no effect of nest-box depth on the predation risk of Blue Tit broods (nest-box depth: $\beta = -0.08 \pm 0.06$, $\chi^2 = 1.78$, df $= 1$, $P =$

TABLE 1. Nest thickness: parameter estimates of a linear mixed model describing the effect of Blue Tit nest-box depth on the thickness of the nest built in the nest box in our study area in the Netherlands. The effect of nest-box depth on nest thickness differered between the experimental years. In the years in which we changed nest-box depth before the breeding season (2011 and 2012), Blue Tits reduced the thickness of their nest in shallower boxes. In the years in which we altered nest-box depth after clutch initiation (2013 and 2014), this effect was absent.

Variable	Estimate ($\beta \pm$ SE)	χ^2	df	P
Intercept	21.59 (4.31)			
Nest-box depth	2.55 (0.37)			
Year				
2012	2.01 (6.48)			
2013	40.99 (10.05)			
2014	34.53 (6.57)			
Nest-box depth × year		16.75	3	<0.001
Nest-box depth × year 2012	−0.38 (0.56)			
Nest-box depth × year 2013	−2.46 (0.75)			
Nest-box depth × year 2014	−1.58 (0.53)			

[a] Rejected terms (for statistics, see text): nest-box depth × plot type (df = 1), plot type (df = 1).

0.18), and no evidence that the effect of nest-box depth differed between the experimental years (nest-box depth × year: $\chi^2 = 5.27$, df = 3, $P = 0.15$).

Adjustment of nest thickness in response to nest-box depth. In the experimental years in which nest-box depth was changed before the breeding season, Blue Tits built thinner nests in the shallower boxes (2011 and 2012; Table 1 and Figure 4). This effect was absent in the experimental years 2013 and 2014, in which we manipulated nest-box depth after clutch initiation (post hoc pairwise comparison of effect of nest-box depth, 2011 vs. 2012: nonsignificant; 2011 vs. 2013: $\beta = −11.26 \pm 2.09$, $t = −5.39$, $P < 0.001$; 2011 vs. 2014: $\beta = −15.43 \pm 1.49$, $t = −10.38$, $P < 0.001$; 2012 vs. 2013: $\beta = −13.81 \pm 2.14$, $t = −6.45$, $P < 0.001$; 2012 vs. 2014: $\beta = −17.98 \pm 1.56$, $t = −11.52$, $P < 0.001$; 2013 vs. 2014: nonsignificant). We found no evidence that the effect of nest-box depth on nest thickness differed between the predation and the non-predation plots (nest-box depth × plot type: predation plot: $\beta = 0.49 \pm 0.41$, $\chi^2 = 1.51$, df = 1, $P = 0.22$). We further found no evidence that nests between predation and non-predation areas differed in their thickness (plot type: predation plot: $\beta = 1.96 \pm 1.15$, $\chi^2 = 2.92$, df = 1, $P = 0.08$).

Nest-Box Depth and Breeding Success of Blue Tit Broods

Clutch size. Nest-box depth had a small but significant positive effect on clutch size (nest-box depth: intercept = 2.18 ± 0.06, $\beta = 0.013 \pm 0.005$, $\chi^2 = 6.47$, df = 1, $P < 0.05$; raw means clutch size [± 95% confidence interval]: 0 block, 10.9 ± 0.3; 1 block, 10.4 ± 0.2; 2 block, 10.0 ± 0.3). This effect was not found to differ between study years or between the predation and non-predation plots (nest-box depth × year: $\chi^2 = 0.63$, df = 3, $P = 0.89$; nest-box depth × plot type, predation plot: $\beta = 0.003 \pm 0.01$, $\chi^2 = 0.11$, df = 1, $P = 0.74$). We found no evidence that clutch size differed between study years or between predation and non-predation plots (year: $\chi^2 = 1.97$, df = 3, $P = 0.58$; plot type, predation plot: $\beta = −0.001 \pm 0.03$, $\chi^2 = 0.001$, df = 1, $P = 0.97$).

Hatching success. Nest-box depth also had a small but significant positive effect on hatching success (nest-box depth: intercept = 1.57 ± 0.20, $\beta = 0.07 \pm 0.01$, $\chi^2 = 26.56$, df = 1, $P < 0.001$; raw means hatching success [with 95% confidence interval]: 0 block, 0.83 [0.81–0.85]; 1 block, 0.82 [0.80–0.83]; 2 block, 0.77 [0.75–0.80]). The effect of nest-box depth did not differ between the study years or between the predation and non-predation plots (nest-box depth × year: $\chi^2 = 2.53$, df = 3, $P = 0.47$; nest-box depth × plot type, predation plot: $\beta = 0.0009 \pm 0.03$, $\chi^2 = 0.0012$, df = 1, $P = 0.97$). We also found no evidence for an effect of clutch size on hatching success ($\beta = 0.019 \pm 0.024$, $\chi^2 = 0.66$, df = 1, $P = 0.41$). Within the same analysis, we did find that hatching success differed between study years (year: $\chi^2 = 130.98$, df = 3, $P < 0.001$). In 2012, 2013, and 2014, hatching success was significantly lower than in 2011 (post hoc multiple comparison, 2012 vs. 2011: $\beta = −1.03 \pm 0.11$, $z = −9.53$, $P < 0.001$; 2013 vs. 2011: $\beta = −1.18 \pm 0.13$, $z = −9.25$, $P < 0.001$; 2014 vs. 2011: $\beta = −0.85 \pm 0.11$, $z = −7.71$, $P < 0.01$; 2013 vs. 2012: nonsignificant; 2014 vs. 2012: nonsignificant; 2014 vs. 2013: nonsignificant). Hatching success was significantly lower in the predation plots than in the non-predation plots (plot type: predation plot: $\beta = −0.60 \pm 0.15$, $\chi^2 = 10.5$, df = 1, $P < 0.01$). To check whether the observed effects of nest-box depth on hatching success were the result of complete brood failure during incubation (potentially as a consequence of actual predation), we reanalyzed the effect of nest box on hatching success including only nests in which ≥1 egg hatched. Effects of nest-box depth on hatching success were slightly smaller but still significant. Moreover, the difference in hatching success between 2011 and the other study years was still apparent. The difference in hatching success between the predation and non-predation plots was no longer significant.

Fledging success. Fledging success increased significantly with nest-box depth in the predation plots, but no such effect was detected in the non-predation plots (Table 2 and Figure 5). We also found that the effect of nest-box depth differed among the experimental study years. Effects of nest-box depth on fledging success were less pronounced in 2011 than in all other study years (post hoc

TABLE 2. Fledging success: parameter estimates of a generalized linear mixed model describing the effect of nest-box depth on the fledging success of Blue Tit broods in our study area in the Netherlands. In plots with high risk of predation (predation plots), nest-box depth had a positive effect on fledging success. This effect was absent in the plots with no or little predation.

Variable	Estimate ($\beta \pm$ SE)	χ^2	df	P
Intercept	6.41 (0.68)			
Nest-box depth	−0.08 (0.05)			
Year				
2012	−3.72 (0.65)			
2013	−4.90 (0.88)			
2014	−1.43 (0.66)			
Plot type				
Predation plot	−4.37 (0.48)			
Brood size	−0.16 (0.03)			
Nest-box depth × year		36.21	3	<0.001
Nest-box depth × year 2012	−0.13 (0.06)			
Nest-box depth × year 2013	−0.20 (0.07)			
Nest-box depth × year 2014	−0.07 (0.05)			
Nest-box depth × plot type		41.29	1	<0.001
Nest-box depth × predation plot	0.21 (0.03)			

TABLE 3. Nest success: parameter estimates of a generalized linear mixed model describing the effect of nest-box depth on the overall probability of nest success in Blue Tits in our study area in the Netherlands. In plots with a high probability of predation (predation plots), the probability of nest success was higher in the deeper nest boxes. This effect was absent in plots with no or little predation.

Variable [a]	Estimate ($\beta \pm$ SE)	Deviance	df	P
Intercept	3.49 (0.84)			
Nest-box depth	−0.03 (0.06)			
Year		36.37	3	<0.001
2012	−1.83 (0.33)			
2013	−1.28 (0.41)			
2014	−1.30 (0.34)			
Plot type				
Predation plot	−4.47 (1.04)			
Nest-box depth × plot type		6.36	1	<0.05
Nest-box depth × predation plot	0.21 (0.08)			

[a] Rejected terms (for statistics, see text): nest-box depth × year (df = 3).

pairwise comparison of the effect of nest-box depth: 2011 vs. 2012: $\beta = 2.13 \pm 0.16$, $z = 13.69$, $P < 0.001$; 2011 vs. 2013: $\beta = 2.55 \pm 0.19$, $z = 13.54$, $P < 0.001$; 2011 vs. 2014: $\beta = 2.22 \pm 0.15$, $z = 15.01$, $P < 0.001$; 2012 vs. 2013: nonsignificant; 2012 vs. 2014: nonsignificant; 2013 vs. 2014: nonsignificant). To check whether the observed effects of nest-box depth on fledging success were the result of complete brood failure during the nestling-rearing phase, we reanalyzed the effect of nest-box depth on fledging success including only broods that fledged ≥1 nestling. We no longer detected any effects of nest-box depth on fledging success. The final model included only study year and brood size.

Number fledged. The slope of the effect of nest-box depth on the number of fledglings produced also differed between the predation and non-predation plots, with a more pronounced positive effect in the predation plots (nest-box depth × plot type: intercept = 2.15 ± 0.14, predation plot: $\beta = 0.05 \pm 0.01$, $\chi^2 = 9.50$, df = 1, $P < 0.01$; Figure 6). We also found that the effect of nest-box depth differed among the experimental study years (nest-box depth × study year: $\chi^2 = 16.63$, df = 3, $P < 0.001$). In 2011, the effect of nest-box depth on the number of fledglings produced was less pronounced than in all other study years (post hoc pairwise comparison of effect of nest-box depth, 2011 vs. 2012: $\beta = 0.39 \pm 0.05$, $z = 8.07$, $P < 0.001$; 2011 vs. 2013: $\beta = 0.53 \pm 0.07$, $z = 7.23$, $P < 0.001$; 2011 vs.

2014: $\beta = 0.41 \pm 0.05$, $z = 8.65$, $P < 0.001$; 2012 vs. 2013: nonsignificant; 2012 vs. 2014: nonsignificant; 2013 vs. 2014: nonsignificant).

Overall nest success. Consistent with the analyses of fledging success and the number of fledglings, the overall probability of nest success increased with nest-box depth, specifically in the predation plots, whereas this effect was absent in the non-predation plots (Table 3 and Figure 7). By contrast, the effect of nest-box depth did not differ between study years ($\chi^2 = 3.72$, df = 3, $P = 0.29$). The overall probability of nest success did differ between study years. In 2011, the probability of nest success was significantly higher than in the other years (post hoc multiple comparison, 2012 vs. 2011: $z = -5.56$, $P < 0.001$; 2013 vs. 2011: $z = -3.14$, $P < 0.001$; 2014 vs. 2011: $z = -3.85$, $P < 0.001$; 2013 vs. 2012: nonsignificant; 2014 vs. 2012: nonsignificant; 2014 vs. 2013: nonsignificant).

The Role of Laying Date

Post hoc, we repeated the analyses of the effects of nest-box depth on nest thickness and the parameters of breeding success, this time including the laying date of the first egg and the interaction between nest-box depth and laying date as predictor variables. This was because in the experimental years in which we changed nest-box depth before Blue Tit nest-box choice, deep boxes were occupied significantly earlier (2011–2012, average laying date, 0 block: April 15; 1 block: April 16; 2 block: April 19; effect of nest-box depth on laying date: linear mixed model, intercept = 23.15 ± 1.36, $\beta = -0.57 \pm 0.11$, $\chi^2 = 24.3$, df = 1, $P < 0.001$). In the experimental years 2013 and

2014, nest-box depth was changed after the first egg was laid and thus the average laying date was not different. Inclusion of laying date and the interaction between nest-box depth and laying date did not change the outcome of our analyses.

DISCUSSION

We found clear positive effects of nest-box depth on breeding success. Blue Tit broods in deeper boxes had a larger clutch size and higher hatching success in all study plots; and, specifically in the study plots with high predation risk, they had higher fledging success, fledgling number, and overall probability of nest success.

Effects of nest-box depth on the overall probability of Blue Tit nest success seemed most pronounced. This is potentially because this measure covered the breeding period from clutch initiation until fledging and thus took into account predation occurring both before and after hatching (40 Blue Tit broods in which laying was initiated were depredated before hatching, and 53 were depredated after hatching). Effects on fledging success were less pronounced than the effects on overall probability of nest success, perhaps because this measure covered predation occurring after hatching only. Interestingly, the slope of the effect of nest-box depth on the number of fledglings in the predation and non-predation areas differed relatively less than in our analyses of fledging success, even though our measure of the number of fledglings covered both the incubation and nestling-rearing periods. Perhaps this is because the number of fledglings produced is the product of clutch size, hatching success, and fledging success. The small but positive effects of nest-box depth on clutch size and hatching success occurred irrespective of local predation pressure, whereas the effects of nest-box depth on fledging success occurred specifically within the predation areas.

We found no indication in any of our analyses that traits of the breeding birds played a role in determining the effect of nest-box depth on breeding success. We did find evidence, in our analyses of fledging success and fledgling number, for a difference in the effect of nest-box depth between the study years. Post hoc analysis showed that 2011 differed from all other study years; thus, there was no clear difference between the free-choice (2011–2012) and forced-choice (2013–2014) experiments. In 2011, predation did not occur as frequently, and this may explain why the effects of nest-box depth on fledging success and the number of fledglings were less pronounced in 2011 than in the other study years in the predation area. The difference in the effect of nest-box depth in 2011 compared to the other years did not show up in our analysis of the overall probability of nest success, perhaps because the latter measure took more predation events into account and,

therefore, the power to discern effects of nest-box depth may have been greater.

Actual Predation vs. Perceived Predation Risk
Predation can affect breeding success both directly, via actual predation; and indirectly, via a behavioral response of the parents, perhaps triggered by their own experience with predation or based on an evolutionary response to predation. Earlier studies on the effects of parents' perception of predation risk on parameters of breeding success in general showed subtle effects (Fontaine and Martin 2006, Lima 2009, Thomson et al. 2012, Hua et al. 2014, Kaliński et al. 2014). These findings suggest that the observed small effects of nest-box depth on clutch size and hatching success in our study, which occurred irrespective of local predation pressure, reflect effects of perceived predation risk on parental investment. In line with this, the small positive effect of nest-box depth on hatching success also remained significant when cases of complete brood failure during incubation, which were potentially due to actual predation, were excluded (further discussed below). The strong positive effects of nest-box depth on fledging success, number of fledglings, and overall probability of nest success, specifically within the areas with high predation risk, may have resulted from a decrease in actual predation with nest-box depth. Actual predation could result in partial or complete brood loss. In our study, complete brood loss due to actual predation seemed to be a main driver of the observed strong effects of nest-box depth on breeding success. Effects of nest-box depth on fledging success disappeared when cases of complete brood loss during the nestling phase were excluded. Further, if we examine brood failure in the period from clutch initiation until fledging, we see that in the predation areas, 47% of the broods failed ($n = 325$), and among the broods that failed, 72% were depredated (based on signs left after predation). In the non-predation areas, 13% of the broods failed ($n = 205$), and among the broods that failed, 10% were depredated. Complete brood failure due to predation thus seems to be a key driver of the effects of nest-box depth on breeding success in our study. However, if actual predation indeed played such a prominent role in determining the effects of nest-box depth on breeding success, why did we not detect any effect of nest-box depth on our measure of the risk of actual predation in the nest boxes?

Measuring effects of nest-box depth on actual predation risk. Quantifying predation risk on the basis of signs left after predation is a method often employed to determine the predation risk at breeding sites of avian species (e.g., Møller 1988, 1989, Wesołowski 2002, Czeszczewik and Walankiewicz 2003, Wesołowski and Rowiński 2012, Kaliński et al. 2014, Berkunsky et al. 2016, Maziarz et al. 2016). The main problem with this method, however, is that predators may be able to successfully depredate broods or breeding parents without leaving any signs (Thompson et al. 1999, Wesołowski et al. 2002, Thompson and Burhans 2004, Pietz et

al. 2012). Data gathered in our study using camera traps on predation of Blue and Great tit broods suggest that martens (*Martes* spp.), presumably the main nest predator in our study area, are able to deprecate nestlings and/or breeding parents without leaving any signs. In 2 of the recorded attempts, the marten was able to snatch 1 or 2 nestlings without leaving any signs (and, thus, during our regular nest-box checks, we would not document that instance of predation; see above). It could also be that other, smaller predators less likely to leave signs after predation (e.g., weasels; Wesołowski 2002) were also preying on broods. We have no evidence from our camera traps that predation by smaller predators occurred. This could be attributable, however, to the camera traps not being sensitive enough to detect smaller mammals (e.g., Marcus Rowcliffe et al. 2011; camera distance from box: 1–3 m). We observed a weasel in one study plot with high predation pressure. Furthermore, one recorded case of predation in this plot cannot be attributed to larger mammals like martens because, in this particular case, nestlings were found to be dismembered within the nest box.

Therefore, by documenting predation risk on the basis of signs left after predation, we may have underestimated the predation that actually occurred. This could explain why we did not detect an effect of nest-box depth on our measure of predation risk but did find clear positive effects of nest-box depth on fledging success, fledgling number, and overall probability of nest success specifically within the areas with high predation risk. It could be that, especially in the shallowest boxes, predators were less prone to leave signs and therefore we found no effect of nest-box depth on predation risk. Unfortunately, the data we gathered with the camera traps were not sufficient to judge this. Overall, this stresses the importance of independent measures of predation risk, for instance using camera traps (see also Weidinger 2010, Pietz et al. 2012).

Effects of nest-site depth on perceived predation risk. Besides actual (but undetected) predation, the more subtle effects of nest-box depth on clutch size and hatching success could potentially be explained by effects of "perceived" predation risk on parental reproductive investment. Several studies have found evidence that parents can lower their investment in reproduction in response to increased perceived predation risk (Fontaine and Martin 2006, Lima 2009, Thomson et al. 2012, Hua et al. 2014, Kaliński et al. 2014). An important example of this work is an experimental study by Fontaine and Martin (2006) in which predators were removed from one area, thus decreasing the nest predation risk, while another area was used as a control. Parents in less safe environments decreased their investment in their offspring as judged by egg size, clutch mass, and feeding rate. One adaptive reason for parents to do so was experimentally shown by Slagsvold (1984), who found that parents with experimen-

tally reduced reproductive effort could renest sooner after their brood was removed and also raised a higher number of fledglings in the renesting attempt compared to parents with increased reproductive effort (see also Martin 1995, Farnsworth and Simons 2001).

Whether parents assess a nest site as having high or low predation risk is potentially dependent on experiences within their lifetime (Lima 2009, Chalfoun and Martin 2010, Ibáñez-Álamo et al. 2015) or on an evolutionary response to predation in the past (Julliard et al. 1997, Sheriff et al. 2010). In our study, the positive effects of nest-box depth on clutch size and hatching success occurred irrespective of local predation pressure. Hatching success was lower in study plots with high predation than in those with no predation, likely as a consequence of brood failure during incubation due to predation (25 of 180 broods failed during incubation in the predation plots, compared to 16 of 309 broods in the non-predation plots), but this effect did not depend on nest-box depth. We thus found no indication that Blue Tit parents in deeper and shallower boxes took local predation risk into account in determining their reproductive investment, based on our measures of clutch size and hatching success. Parents may instead have responded to the "potential" higher predation risk in shallower boxes. That parents are likely aware of the depth of their box and the related predation risk is shown by the fact that parents reduced the thickness of their nest in the shallower boxes (see also Mazgajski and Rykowska 2008, Kaliński et al. 2014). This effect also occurred irrespective of local predation pressure. Changing nest-box depth after the first egg was laid did not trigger nest-thickness adjustments by the parents (forced-choice experiment). This shows that although, during nest building, birds still adjusted the thickness of their nest to the depth of their nesting cavity, this was no longer done after the nest was completed. Parents may trade off the potential fitness loss due to a thinner nest (e.g., reduced thermoregulation) with potential fitness loss due to higher nest predation (Heenan 2013, Kaliński et al. 2014, Mainwaring et al. 2014). The observed positive effects of nest-box depth on nest thickness may (in part) explain the observed positive effects of nest-box depth on hatching success. However, within the analysis of the effect of nest-box depth on hatching success, we did not detect a difference in the effects of nest-box depth between the study years, whereas in the analysis of the effect of nest thickness we did find a difference. Overall, in our study, parents seem to have perceived the shallower boxes as more risky and may have adjusted their reproductive investment accordingly. We judge that the subtle effects of nest-box depth on clutch size and hatching success, especially, are likely a reflection of effects of nest-box depth on parental investment. The strong effects of nest-box depth on fledging success, fledgling number, and

overall probability of nest success were likely driven by complete brood failure due to actual predation.

Conclusion

In a previous study, we found evidence that Blue Tits (as well as Great Tits) in our study area prefer deeper nest sites over shallower ones (R. W. Fokkema et al. personal observation). These findings were in line with those of earlier studies indicating that other cavity-breeding species breed more readily in deeper cavities (van Balen 1984, Löhrl 1986, Aitken et al. 2002, Wesołowski 2002, Mazgajski 2003, Maziarz et al. 2015, 2016). Here, we have experimentally shown that nest-site depth, independent of variation in parental quality, positively affects the breeding success of Blue Tits. The observed fitness effects of nest-site depth were most pronounced in areas with high predation. Besides evidence of decreased actual predation with nest-box depth, we also found indications that parents perceive shallower nest sites in general as more risky and adjust their nest thickness and reproductive investment accordingly. Our results thus demonstrate that both actual predation and effects of perceived predation risk on the reproductive investment of parents can shape the nesting preference of Blue Tits for deeper cavities.

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