# Patterns of predator behaviour and Wood Warbler *Phylloscopus sibilatrix* nest survival in a primaeval forest

MARTA MAZIARZ,[1,2,3]* (iD) ALEX GRENDELMEIER,[1] TOMASZ WESOŁOWSKI,[3] RAPHAËL ARLETTAZ,[4,5]
RICHARD K. BROUGHTON[6] (iD) & GILBERTO PASINELLI[1] (iD)
[1]*Swiss Ornithological Institute, Seerose 1, CH-6204, Sempach, Switzerland*
[2]*Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00 679 Warsaw, Poland*
[3]*Laboratory of Forest Biology, Wrocław University, Sienkiewicza 21, 50 335 Wrocław, Poland*
[4]*Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern,
Switzerland*
[5]*Swiss Ornithological Institute, Valais Field Station, rue du Rhône 11, 1950 Sion, Switzerland*
[6]*Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, OX10 8BB, UK*

Understanding the foraging behaviour of predators is key to interpreting the role of anti-predator adaptations of birds in reducing nest losses. Conducting research in primaeval habitats, with a low level of direct human interference, is particularly valuable in the understanding of predator–prey interactions. Using nest cameras, we investigated the identity and behaviour of potential and actual predators appearing at Wood Warbler *Phylloscopus sibilatrix* nests, and the importance of different predator groups for nest survival, in the primaeval part of Białowieża Forest (Poland). Mammals formed the main predator group (30 of 32 nest depredations), particularly medium-sized carnivores (24 of 32), which attacked nests more frequently than merely passing by. This contrasted with other species, especially small rodents, which were commonly recorded near nests but rarely attacked them. Most nest attacks (22 of 32) took place at night and nest survival did not depend on nest visibility, indicating a reduced utility of nest concealment in defence against predators using mainly sound or olfaction when hunting. Daily nest survival declined strongly with nest progression (from egg-laying to fledging of chicks), probably due to increased predator detection of nests containing older and louder chicks, rather than to increasing parental activity at nests during the day. The set of actual nest predators differed from some previous studies in human-transformed habitats, showing that Wood Warblers may face different threats in modified vs. near-pristine environments.

**Keywords:** Białowieża Forest, camera traps, predation, songbird.

Predation is a major selective force shaping the evolution of animals, and the dominant cause of breeding failure in birds. To survive and reproduce, songbirds (Passeriformes) have evolved various behavioural and morphological adaptations to minimize the hunting efficacy of predators plundering their nests (e.g. Edmunds 1974, Lima & Dill 1990,

Lima 2009). As different nest predators employ various hunting methods, the overall threat posed to nesting birds depends on the diversity and individual abundance of species among the local predator community (e.g. Picman & Schriml 1994, Thompson 2007, Weidinger 2010). To understand and interpret correctly the anti-predator adaptations of birds, it is necessary to determine the identity and foraging behaviour of the nest predators.

In ecosystems that are significantly modified by humans, such as secondary forests, predator

*Corresponding author.
Email: mart.ann.maz@gmail.com
Twitter: @woodlandeco

species composition may differ from that of primaeval conditions (Tomiałojć *et al.* 1984). Human persecution typically results in an impoverished predator fauna in managed forests (Reynolds & Tapper 1996), although some predators may benefit from human activities and increase their abundance beyond that seen in natural forests (Andrén *et al.* 1985, Thompson 2007). As such, conclusions inferred from predator–prey dynamics based only on studies from modified habitats may not be representative of the selection pressures that produced current anti-predator adaptations, due to differences in the predator community between pristine and altered habitats.

Primaeval forests, comprising old-growth stands with minimal direct human impact, have survived in only a few places in Europe, including the strictly protected region (47 km$^2$) within the Białowieża National Park (hereafter BNP) in eastern Poland (for a definition and detailed description see Tomiałojć *et al.* 1984, Tomialojc 1991, Tomiałojć & Wesołowski 2004). These forest stands represent a relic of the lowland mixed-deciduous forests that formerly covered much of temperate Europe (Wesołowski 2007). The predator fauna of BNP consists of at least 30 species of birds and mammals which habitually depredate birds and/or their nests (Tomiałojć *et al.* 1984). This predator community comprises diurnal and nocturnal species that use a variety of methods for nest detection and attack, including vision, olfaction and sound, and pose a substantial threat to avian prey species (Wesołowski & Tomiałojć 2005).

Prior research on the predators attacking camera-monitored bird nests comes mostly from fragmented, secondary forests (e.g. Schaefer 2004, Weidinger 2010, Mallord *et al.* 2012, Grendelmeier *et al.* 2015, Bellamy *et al.* 2018, Maziarz *et al.* 2018) and comparable data are lacking from temperate habitats with little human interference. Thus, it is unknown whether the nest predators documented so far are representative of the primaeval conditions in which the bird adaptations have evolved. Furthermore, there are no data documenting the incidence of predators passing close to bird nests but not attacking them. Therefore, it is difficult to draw conclusions regarding the potential risk posed by different species to nesting birds in relation to the success of avian behavioural adaptations in evading the threat of predation.

We investigated patterns of Wood Warbler *Phylloscopus sibilatrix* nest predation in the temperate primaeval forest of BNP using cameras to record the identity, incidence and behaviour at nests of individual species from among the diverse predator community. First, we predicted that predator species would differ in their efficacy to predate nests, and that efficient species would attack nests more often than merely passing by them. We addressed this prediction by quantifying the relative incidence of small rodents, carnivores and other potential predators passing by Wood Warbler nests, and the frequency of their respective nest attacks.

Secondly, we tested whether the diel pattern of nest predation depended on the predator species (e.g. Benson *et al.* 2010, Weidinger 2010). If visually oriented species (e.g. diurnal birds) were the main nest predators, Wood Warbler nests would be primarily predated during daylight hours. Alternatively, if species mainly relying on sound or olfaction (most mammals) to detect prey were the most frequent nest predators, then nocturnal attacks would dominate. We presumed that visually oriented predators would be most efficient in detecting the nests during daylight hours, whereas predators using mainly sound or olfaction for prey detection would also efficiently hunt their prey at night. If correct, visually oriented predators would attack the nests more often than merely passing by them during daylight hours, whereas the opposite daily pattern would be expected for species using mainly sound or olfaction for prey detection.

Thirdly, if visually oriented predators predominated, Wood Warblers would be able to mitigate the threat by concealing their nests. Consequently, nest survival would decrease with nest visibility (Grendelmeier *et al.* 2015). In contrast, if mammalian predation predominated, nest survival would be unrelated to nest visibility, as hiding the nest would be ineffective in impairing its detection by predators that use sound or olfaction to hunt prey (e.g. Holway 1991, Pietz & Granfors 2000).

Finally, we evaluated whether survival of nests monitored with cameras differed from those monitored without them and tested other factors that were previously found to influence Wood Warbler nest survival (Wesołowski 1985, Wesołowski & Maziarz 2009, Mallord *et al.* 2012, Grendelmeier *et al.* 2015). Nest progression (from egg-laying to fledging of chicks) is generally associated with increasing parental activity over time that may

attract predators (Martin *et al.* 2000, Zanette *et al.* 2011), so we expected reduced nest survival in the later stages of nesting. We further hypothesized that the relationship between nest survival and nest visibility might vary between habitat types, study plots and years, or in relation to the timing of breeding (e.g. between early and late breeding attempts) due, for example, to possible spatial and temporal variation in predator abundance and/or activity (Thompson & Burhans 2003, Benson *et al.* 2010). We therefore assessed the importance of the interactions between nest visibility and these factors in explaining variation in nest survival.

## METHODS

The Wood Warbler is a small (10 g) songbird that breeds in temperate European forests. Immediately after arrival in April or early May from wintering grounds in equatorial Africa, females construct a well-camouflaged nest consisting of a cup of woven grass and animal hair, and a domed roof of leaves and grass (Cramp 1992). The nest is situated in a scrape on the forest floor, hidden among herbs and grasses (Wesołowski 1985), but easily accessible to all potential nest predators. Consequently, predation constitutes the main cause of Wood Warbler nest failure, accounting for 79–95% of losses (Wesołowski 1985, Wesołowski & Maziarz 2009, Mallord *et al.* 2012, Grendelmeier *et al.* 2015, Bellamy *et al.* 2018).

### Study site

The study was conducted in 2015 and 2016 mainly within three permanent plots situated in the strictly protected area within BNP (52°29′–52°57′N, 23°31′–24°21′E), distributed 1–2 km apart. Two of the plots, M (54 ha) and W (50 ha), contain stands of mostly Hornbeam *Carpinus betulus*, Small-leaved Lime *Tilia cordata*, Pedunculate Oak *Quercus robur*, Norway Spruce *Picea abies* and Norway Maple *Acer platanoides*. The soil is usually dry to moist with a predominantly moderate and low (0–0.5 m) herb layer and a sparse shrub layer. The third plot, N (50 ha), consists of mixed-coniferous stands of Norway Spruce and Scots Pine *Pinus sylvestris* with an admixture of mature birch *Betula* spp. and Pedunculate Oak, and some patches of young deciduous trees. The soil is sandy and dry with a relatively sparse herb layer and few shrubs. Fallen logs and branches are frequent in plots M and W, and superabundant in plot N. For a detailed description of the plots see Tomiałojć *et al.* (1984) and Wesołowski *et al.* (2015).

### Nesting data

Searches for Wood Warbler nests were performed between early May and mid-July during daily visits to the plots. Approximately 80–90% of all nests that were initiated in 2015 and 2016 were located, based on the number of recorded territories and male behaviour indicating pairing (Cramp 1992). Nests found $c. \geq 1$ km outside of the plots in the same habitat types were also included in the analyses and constituted 9% of the 176 nests found.

Nests were mostly (64%) found at the building or egg-laying stages. They were typically inspected every 3–5 days (range 1–9 days) until young fledged or the nest failed, to determine the dates of egg-laying, hatching, fledging and the nest outcome. For nests found after incubation had commenced, laying date was back-calculated by assessing embryo development by 'candling' (Ojanen & Orell 1978) and hatching date by the nestling growth stage (Wesołowski & Maziarz 2009). Calculations assumed one egg was laid per day, clutches consisted of six eggs, an incubation period of 13 days beginning with laying of the last egg, and a nestling period of 13 days after hatching. The clutch size and duration of the incubation and nestling periods corresponded to the median values in BNP (Wesołowski & Maziarz 2009, M. Maziarz unpubl. data).

To identify predators and record their behaviour at nests, we used PC900 HyperFire Professional High Output Covert camera traps (dimensions: $14 \times 11 \times 8$ cm; Reconyx Inc., Holmen, WI, USA), which incorporated 'no glow' infrared technology that produced no visible light during activation (Reconyx, Inc. 2013). The cameras were deployed at 39 nests during the egg-laying or incubation stages, distributed evenly across the plots. Nests were monitored continuously until nest failure or fledging of the young, when cameras could be re-deployed at other active nests at various stages, giving 85 camera-monitored nests in total ($n = 34$ in plot M, $n = 23$ in plot N, $n = 21$ in plot W and $n = 7$ outwith the plots). Cameras were installed $c.$ 1 m from a nest, typically mounted 0.6 m above ground on wooden stakes and positioned to provide a 1- to 2-m field

of view of the nest entrance and its immediate surroundings. Cameras were programmed to capture 10 images at 1-s intervals when triggered (0.5 s trigger speed reported by the manufacturer), with one control image every 15 min (time-lapse setting). Cameras were visited for several minutes every 3–6 days to check and/or replace batteries and memory cards, which usually coincided with the nest check to minimize observer visits at nests. No nest desertions occurred due to camera installation.

Once nestlings were 10 days old (day of hatching = day 0) and capable of escaping predators (Wesołowski & Maziarz 2009), all nests were checked daily from a distance to avoid premature fledging. Breeding attempts were treated as successful if a camera recorded the young leaving the nest. In cases where fledging was not recorded, or for nests without cameras, success was inferred if fresh droppings of young that were aged 10–12 days old were present next to the nest and/or fledglings or an adult carrying food was found nearby. In the absence of such signs on a minimum of two visits (of 30–60 min), the breeding attempt was treated as a failure along with nests that were destroyed or when the contents disappeared before young were 10 days old.

Causes of failure at nests monitored with cameras were based on picture evidence. At nests where the evidence was unclear, and those not monitored by cameras, causes of failure were based on descriptions of the nest and surroundings, and classified as 'predation' or other causes of nest failure (Table 1).

## Nest visibility

To examine the impact of nest visibility on nest survival, this characteristic was recorded within several days of finding each nest, mainly during the egg-laying and incubation period (105 of 162 nests), and less frequently at the hatching (20 nests), nestling (26) or post-fledging (11) stages.

The visibility of each nest was assessed by a human observer from 20 to 30 cm above the ground (i.e. at the approximate height of a medium-sized predator) standing about 1.5 m from the nest, classified as '0' if the nest was mostly/completely hidden, '0.5' if approximately 50% of the nest was visible or '1' if mostly/fully visible. The scores were taken from five angles: entrance, right and left sides, back and top of the nest, and

**Table 1.** Classification of causes of nest failure in Wood Warblers based on descriptions of nests and their surroundings.

| Cause | Description |
|---|---|
| Predation | Nest torn apart or with enlarged entrance or otherwise intact but empty prior to the expected fledging date or containing remnants of eggs, nestlings and/or an adult |
| Desertion | No signs of predation, the contents and the nest intact |
| Desertion due to parasitism | By Common Cuckoo *Cuculus canorus*; cold eggs of Wood Warbler and Cuckoo egg in an intact nest |
| Eggs failed to hatch | The nest deserted after a prolonged incubation period lasting more than 17 days |
| Trampling | A crushed nest containing destroyed eggs or dead young |

summed to obtain the index of nest visibility. The index ranged from '0' when the nest was invisible from all angles to '5' when the nest was fully visible from all sides all around.

## Predator data analyses

To test whether the recorded nest predator species differed in their efficacy to detect nests, we compared the incidence of potential predator species passing by the nests and not attacking them with the corresponding incidence of actual attacks. For this purpose, we used a two-tailed Fisher exact test. We classified potential predators as all species of animals that were previously recorded in the literature predating nests of Wood Warblers or other bird species, but that in this instance passed in the vicinity of nests and did not actually attack them. In the analyses, we included only the cases when potential predators came within approximately 1 m of an active camera-monitored nest. We grouped the potential predators into small rodents, carnivores and 'other' species (Tables S1 and S2) to investigate which group posed the greatest threat to Wood Warbler nests.

To investigate the diel pattern of nest predation, the occurrence and behaviour of potential predators (i.e. passing by but not attacking) and actual predators (i.e. attacking the nests) was recorded with the date and time stamped on the images. The images were later classified according to the predator group (small rodents, carnivores, other species), presence of an adult warbler in the nest (present/absent) and time of day. The last of these

was used to assign events at the nest as occurring during the 'day' (sunrise to sunset where sunrise from May until mid-July was between 04:05 and 04:53 h local time, UTC + 2 h, and sunset between 19:51 and 20:50 h) or during the 'night' (sunset to sunrise). To investigate the hunting efficacy of predators that mostly relied on vision, olfaction and/or sound when attacking the nests, we used a two-tailed Fisher exact test that assessed the difference in the number of events when predators were passing or attacking the nests in relation to day or night.

We used generalized linear mixed-effects models (GLMMs) with a logit link function and binomial error structure to test whether the likelihood of a nest being attacked (including cases when at least one young survived) or passed within 1 m by a predator (response variable) was related to nest visibility. In the analysis, nest identity was included as a random effect to account for the inter-dependency arising from using multiple observations per nest when potential predators sequentially appeared at the same nests. We used a generalized linear model (GLM) with a logit link function and binomial error structure to test whether the likelihood of a nest being attacked or not (response variable) depended on the number of events of potential predators passing by the nests (including cases when no potential predator was recorded).

## Nest survival analyses

Survival analyses included all nests in which egg-laying had commenced and from which the outcome (successful or failed) and nest visibility was known ($n = 157$ nests). To analyse nest survival, we used the logistic-exposure method (Shaffer 2004, Grant *et al.* 2005) and considered the number of days a nest was known to be active (hereafter referred to as nest exposure), thereby accounting for the number of days a nest was exposed to predators and other threats. The duration of nest exposure lasted from the day of finding the nest or, for those found during building, the day that the first egg was laid, until nest failure or fledging of the chicks (Mayfield 1961, Hazler 2004). For nests with cameras, the dates of fledging and failure were recorded directly. For nests without cameras, or if fledging was not recorded on camera, fledging date was the day on which a nest was found to be empty after being active on the previous day. The date of nest failure was

assessed with an accuracy of 1–5 days and corresponded to the median date between visits when the nest was found to have been lost and when it was last active (Hazler 2004).

For each nest, its survival was coded and modelled as a binary response variable ('1' if still active or successful, '0' if failed) on a day-by-day basis using a logit link function and binomial error structure with GLMMs. Hence, each nest provided multiple data points, and we accounted for this dependency with a random effect of nest identity.

We tested whether survival of nests monitored with cameras differed from those monitored without them, and whether nest survival was related to nest visibility. Additionally, we tested how factors such as habitat type (mixed-coniferous or deciduous stands), study plot (M, N, W, Other), study year (2015 or 2016), timing of breeding (relative 1st egg date corresponding to the number of days from the annual median of egg-laying commencement) and/or nest progression (the number of days since the first egg was laid until fledging or failure) might have affected the relationship between nest survival and nest visibility. A detailed description of all explanatory variables is included in Table S3. To test whether nest survival decreased with increasing nest visibility, we treated the nest visibility index as a linear variable. All continuous variables were z-transformed prior to analysis.

Using the dredge function in the MuMIn package (Bartoń 2018), we created a set of candidate models represented by GLMMs as specified above. We selected a subset of models that all contained nest visibility index (fixed effect) with all possible (additive) combinations of other factors (all fixed effects), such as habitat type, study plot, study year and timing of breeding (relative 1st egg date). Presuming a strong decline of nest survival with nest progression (Wesołowski 1985, Mallord *et al.* 2012, Grendelmeier *et al.* 2015), we added the linear (fixed) effect of nest progression in all models, including the null model. Next, models with interactions were added to test whether the potential effect of nest visibility on nest survival differed over space and time. In addition to nest progression (see above), these models contained the main effects and interactions of nest visibility and (1) habitat type, (2) study plot, (3) study year, (4) the linear (fixed) effect of relative 1st egg date or (5) the interaction of nest progression (after confirming that the models with linear effects were more parsimonious than models with quadratic effects).

Finally, we added a model containing additive (fixed) effects of camera presence and nest progression, and the 'null' model containing only a fixed effect of nest progression

We merged all of these 23 candidate models and performed model selection across all of them using the MuMIn package. Candidate models were ranked by the small-sample-size corrected version of Akaike's information criterion (AICc), with the most parsimonious (and best supported) model being indicated by the lowest AICc value. To account for model selection uncertainty (Burnham & Anderson 2002), estimates and 95% confidence intervals (CI) of all variables were calculated by model averaging across all candidate models.

Daily nest survival rates were calculated for the 31-day nesting period (the median duration in our study) using the inverse logit distribution function of the bootstrapped (10 000 replicates) intercept and estimate of the top model, produced by the GLMM (lme4 and arm packages; Bates *et al.* 2015, Gelman & Su 2016).

All statistical analyses were performed in R version 3.4.4 (The R Core Team 2018).

## RESULTS

### Predator behaviour recorded at camera-monitored nests

A potential predator was recorded passing by, but not attacking, 40 of 85 camera-monitored nests. This occurred from once (17 of 40 nests) to up to five times (three cases) at an individual nest and involved between one (28 of 40 nests) and three (four cases) potential predator species. In total, 11 species of potential predators were recorded by cameras (Table 2). At 23 of the 85 nests no predator was recorded, but five of these nests failed due to Common Cuckoo *Cuculus canorus* parasitism ($n = 3$) or desertion ($n = 2$).

Non-attacking predators detected by cameras at 40 nests appeared to be foraging nearby in 26 of 87 incidences. Occasionally a Yellow-necked Mouse *Apodemus flavicollis* (four events) inspected a nest containing chicks aged $\geq 8$ days, or a Pine Marten *Martes martes* (two events) investigated the nest containing a brooding Warbler parent or nestlings aged 8 days, but did not attack (see example in Fig. S1a). Of 26 cases where a potential predator passed by or over a nest containing an adult Warbler sitting inside (presumably

**Table 2.** The number of events and camera-monitored Wood Warbler nests at which different predator species were recorded passing or attacking. The events of the same potential predator species passing a nest were separated by at least 20 min. The numbers obtained from each study plot and year are shown in Tables S1 and S2.

| Species | Predator passing | | Predator attacking |
|---|---|---|---|
| | *n* Nests | *n* Events | *n* Events |
| *Dendrocopos major* | 3 | 5 | 2 |
| *Sciurus vulgaris* | 5 | 5 | 2 |
| *Myodes glareolus* | 5 | 10 | 1 |
| *Apodemus flavicollis* | 17 | 39 | 1 |
| *Apodemus/ Myodes* spp. | 1 | 1 | 0 |
| *Nyctereutes procyonoides* | 0 | 0 | 1 |
| *Vulpes vulpes* | 8 | 10 | 15 |
| *Martes martes* | 5 | 5 | 7 |
| *Meles meles* | 1 | 1 | 1 |
| *Sus scrofa* | 8 | 8 | 2 |
| Other[a] | 3 | 3 | 0 |
| Unknown[b] | – | – | 4 |

[a]*Grus grus*, *Glaucidium passerinum*, *Garrulus glandarius*.
[b]The predator was not caught by the camera, but predation was indicated by traces such as empty nest when young were present, damaged eggs or killed young.

females, which incubate the eggs and brood young alone; Cramp 1992), only two birds fled; the others sat tightly throughout the encounter (see example in Fig. S1b).

Cameras recorded actual attacks at 36 of 85 nests, identifying nine predator species at 32 of these (Table 2; see examples in Fig. S2). Five recorded attacks involved the same predator species that had previously been recorded passing the nest. Another five attacks involved a different species from that initially detected, and four attackers were unidentified at nests where a potential predator had previously been recorded passing by. Whether a nest was attacked or not did not depend on the number of cases when potential predators passed the nests (GLM, estimate = $0.040 \pm 0.22$ se, $P = 0.86$), with an average of $1.1 \pm 1.6$ sd ($n = 36$ individual nests) cases for attacked and $1.0 \pm 1.3$ sd ($n = 49$) cases for nests that were not attacked. Of 10 attacks, an adult Warbler within the nest managed to escape at the last moment in eight cases, but two others were probably caught by the predator. In six attacked nests containing young aged 10–12 days, at least one chick managed to escape.

Carnivores, mainly Red Fox *Vulpes vulpes* and Pine Marten, were recorded attacking the nests most often (Table 2). Compared with small rodents (*Apodemus* or *Myodes* spp.) and other species, this set of main predators depredated nests (24 of all 32 attacks) significantly more often than merely passing them (16 of all 87 events; Fisher exact test, $P < 0.001$; Table 2). In contrast, small rodents only occasionally attacked nests (2 of 32 attacks), and did so significantly less often than just appearing nearby relative to all other predators (50 of 87 events; Fisher exact test, $P < 0.001$; Table 2). The attacks included a Yellow-necked Mouse recorded killing and removing chicks from a nest and a Bank Vole *Myodes glareolus* repeatedly disturbing a nest during the night, followed by the disappearance of the female Warbler and eggs by the next nest check. Compared with carnivores and small rodents, other predators attacked nests at a similar frequency as passing by them (Fisher exact, test $P = 0.63$; Table 2).

In total, 30 of 32 recorded attacks involved mammals, with the only avian predator being a Great Spotted Woodpecker *Dendrocopos major* (Table 2). The majority of recorded nest attacks (22 of 32) took place at night, and were mainly by carnivores (18 of 22 nocturnal attacks by all species; Fig. 1). The frequency of carnivores attacking nests was greater at night (18 of 24 carnivore attacks) than during the day, which contrasted with their incidence of passing by a nest (10 diurnal occurrences among 16 events; Fisher exact test, $P = 0.025$; Fig. 1).

The chances of a nest being attacked or passed by a predator did not depend on nest visibility (GLMM, estimate = $0.050 \pm 0.14$ se, $P = 0.73$). After excluding the 14 nests which were both passed and attacked, the nest visibility index averaged $1.83 \pm 1.41$ sd ($n = 20$ individual nests) for attacked nests and $1.79 \pm 1.35$ sd ($n = 24$) for nests that were passed by.

## Factors affecting nest survival

In 2015 and 2016, 81 of 176 Wood Warbler nests failed, with predation being the major cause (64 of 81 failed attempts). Minor causes of nest failure included trampling by Wild Boar *Sus scrofa* or another unrecorded animal (two cases), failure of eggs to hatch (three cases), Cuckoo parasitism (four cases) and desertion (eight cases). At least two cases of desertion probably were also caused
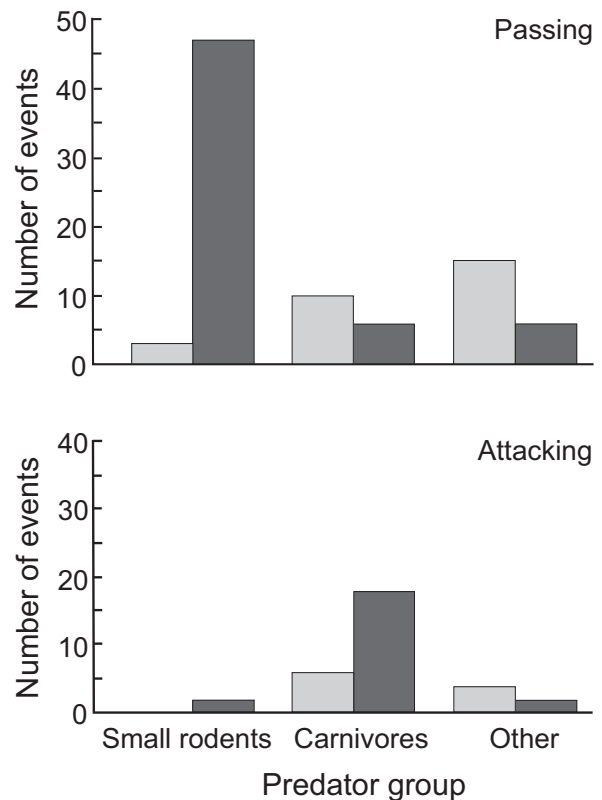


**Figure 1.** Number of events when a small rodent, carnivore or other potential predator was passing ($n = 87$) or attacking ($n = 32$) a Wood Warbler nest during the day (light grey) and night (dark grey) in 2015–2016 based on nest cameras. Species classified into the three groups of predators are listed in Tables S1 and S2, and examples of predators passing by and attacking nests are given in Figs S1 and S2.

by a predator's presence/attack, as indicated by field signs (presence of Wood Warbler tail feather at the nest entrance) and camera imagery (disappearance of an incubating female after nest investigation by a Pine Marten).

Nest survival was unrelated to the presence or absence of a camera at nests, indicating that it did not influence predator behaviour. Although the ΔAICc of the model containing the factor 'camera' was < 2 relative to the top model, the 95% CI of the estimate for this variable overlapped with zero (Tables 3 and 4). Furthermore, nest survival of all monitored nests was unrelated to nest visibility, with the null model being the top one and the 95% CI of the estimate for nest visibility index overlapping with zero (Tables 3 and 4; the proportions of predated and all nests in relation to nest visibility are shown in Fig. 2).

**Table 3.** Results of model selection showing the effects of nest visibility and other temporal and environmental variables on daily Wood Warbler nest survival rate. Models with ΔAICc ≤ 2, with nest outcome (successful/failed) as a response variable, are shown. $w_i$ = AIC weights, $n$ = 157 nests (19 nests had to be excluded due to missing information on nest visibility). For a description of all variables, see Table S3.

| Model | K | AICc | ΔAICc | $w_i$ | Log-likelihood |
|---|---|---|---|---|---|
| Nest progression[a] | 2 | 617.47 | 0.00 | 0.19 | −306.73 |
| Nest progression + nest visibility + nest visibility × nest progression | 4 | 618.80 | 1.33 | 0.10 | −305.39 |
| Nest progression + nest visibility + study plot | 6 | 619.23 | 1.75 | 0.08 | −303.60 |
| Nest progression + camera presence | 3 | 619.30 | 1.83 | 0.08 | −306.65 |
| Nest progression + nest visibility | 3 | 619.47 | 2.00 | 0.07 | −306.73 |

[a]Number of days since the first egg was laid (= day 1) until fledging or nest failure.

**Table 4.** Results of model-averaged estimates, standard errors (se) and 95% confidence intervals (CI) across all models assessing daily Wood Warbler nest survival rate ($n$ = 157 nests; 19 nests had to be excluded due to missing information on nest visibility). For a description of all variables, see Table S3.

| Variable | Estimate | se | 95% CI Lower | 95% CI Upper |
|---|---|---|---|---|
| Intercept | 4.155 | 0.39 | 3.39 | 4.92 |
| Nest progression[a] | −0.689 | 0.14 | −0.97 | −0.41 |
| Nest visibility | −0.033 | 0.13 | −0.34 | 0.25 |
| Nest visibility × nest progression | 0.022 | 0.08 | −0.04 | 0.49 |
| Study plot | | | | |
| N | −0.067 | 0.34 | −1.36 | 0.93 |
| W | −0.215 | 0.36 | −1.27 | −0.11 |
| Other | −0.045 | 0.44 | −1.37 | 1.66 |
| Camera (present) | 0.008 | 0.08 | −0.39 | 0.60 |
| Timing of breeding[b] | −0.038 | 0.09 | −0.38 | 0.09 |
| Habitat type (deciduous) | 0.088 | 0.34 | −0.86 | 1.77 |
| Nest visibility × timing of breeding | −0.006 | 0.04 | −0.41 | 0.12 |
| Year (2016) | −0.011 | 0.12 | −0.63 | 0.50 |
| Nest visibility × study plot N | 0.009 | 0.08 | −0.33 | 1.00 |
| Nest visibility × study plot W | −0.005 | 0.06 | −0.78 | 0.36 |
| Nest visibility × study plot Other | 0.034 | 0.31 | −1.49 | 4.10 |
| Nest visibility × habitat type (deciduous) | 0.000 | 0.04 | −0.65 | 0.69 |
| Nest visibility × year (2016) | 0.000 | 0.03 | −0.68 | 0.59 |

[a]Number of days since the first egg was laid (= day 1) until fledging or nest failure. [b]Relative 1st egg date (days from median of a year).

The relationship between nest survival and nest visibility was not affected by year, habitat type, study plot or timing of breeding, as the ΔAICc of models containing the interactions between nest visibility and these variables was always > 2 compared with the top model (Table 3; the number of predated, otherwise failed and successful nests in different study plots, habitats, years and in relation to timing of breeding is given in Table 5). Although a well-supported model (with ΔAICc ≤ 2) included the interaction between nest visibility index and nest progression (Table 3), the 95% CI of the estimate for this interaction overlapped with 0 (Table 4).

Nest survival decreased strongly with nest progression (Fig. 3), however, which featured in the top model, and the 95% CI of the estimate for nest progression was below 0 (Tables 3 and 4). Based on this model, daily nest survival averaged 0.980 (95% CI 0.948–0.996) over all 157 nests that were successful or failed, and mean nest survival for the 31-day nesting period was 0.536 (95% CI 0.423–0.642). Nest survival was also lowest in plot W (Table 4).
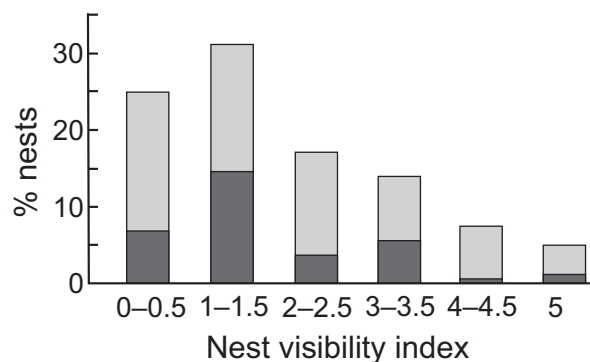
**Figure 2.** The percentage of all Wood Warbler nests (light grey) and of predated nests included within this total (dark grey, $n = 52$ of 157) with different visibility indices in 2015–2016. The index was based on scores taken $c$. 1.5 m from the nest and $c$. 20–30 cm above the ground from five angles: entrance hole, right and left sides, back, and top of the nest; score 0 = nest wholly or mostly invisible, 0.5 = approximately 50% of the nest visible, 1 = the nest mostly or fully visible. The five scores per nest were summed, resulting in an index ranging from 0 to 5.

## DISCUSSION

The results from camera-monitoring of ground-nesting Wood Warblers in BNP showed that predator species differed in their efficacy to detect and attack nests. Carnivores, particularly foxes and martens, were the most common nest predators, forming the only group that attacked nests more often than appearing nearby. In contrast, small rodents, such as mice or voles, were the most frequently recorded at nests, but their nest attacks were rare. Other predator species attacked nests at a similar frequency to passing them by. These findings indicated that carnivores posed the greatest direct threat to ground-nesting Wood Warblers by being particularly effective in predating the nests, while the direct risk from other species, including small rodents, was negligible.

By observing nests in widely distributed plots and additional nests located outside of them, we aimed to minimize any potential bias of recording the same individual predators at multiple nests within their large home-ranges (Goszczyński 2002, Zalewski *et al.* 2004). Despite this, the high frequency of a Red Fox passing and attacking Wood Warbler nests in one plot (M) in 2016 (Tables S1 and S2) suggested a single animal whose home-range covered much of the plot and that was particularly successful in predating Wood Warbler

**Table 5.** The number of Wood Warbler nests predated, failed due to causes other than predation, or successful in relation to habitat type, study plot, year, timing of breeding (nesting early vs. median vs. late; median 1st egg date was 15 May in 2015 and 10 May in 2016) and camera presence. For a description of all variables, see Table S3.

| Variable | Number of nests | | |
|---|---|---|---|
| | Predated | Other failed | Successful |
| Habitat type | | | |
| Coniferous | 8 | 6 | 14 |
| Deciduous | 56 | 11 | 81 |
| Study plot | | | |
| M | 19 | 5 | 42 |
| N | 10 | 6 | 19 |
| W | 29 | 6 | 25 |
| Outside | 6 | 0 | 9 |
| Year | | | |
| 2015 | 33 | 4 | 45 |
| 2016 | 31 | 13 | 50 |
| Timing of breeding (relative 1st egg date) | | | |
| Early ($< -2$) | 21 | 4 | 34 |
| Median (from $-2$ to 2) | 28 | 6 | 30 |
| Late ($> 2$) | 15 | 7 | 31 |
| Camera | | | |
| Present | 29 | 8 | 48 |
| Absent | 35 | 9 | 47 |

nests. Nevertheless, carnivore predation may have also been under-recorded in other study plots, where there were fewer camera traps than in plot M (see Methods). This may include plot W, where nest predation was highest and the remains of nests unmonitored by cameras suggested frequent predation by carnivores (M. Maziarz unpubl. data). The relatively common records of Yellow-necked Mice passing nests in plot W (Tables S1 and S2) may reflect a locally higher density of these animals. These potential biases did not appear greatly to have affected the observed patterns of Wood Warbler nest survival, however, which was similar for camera-monitored and other nests. The ratio of the number of events of predator species passing and attacking nests in different study plots was also comparable. Thus, the results for the frequency of predator species recorded at nests were considered a reliable indicator of predator activity and the specific threats posed to ground-nesting birds (Schmidt *et al.* 2006).

Our study supports the low incidence of nest predation by small rodents found in nest camera studies elsewhere (Mallord *et al.* 2012, Grendelmeier *et al.* 2015, Bellamy *et al.* 2018, Maziarz
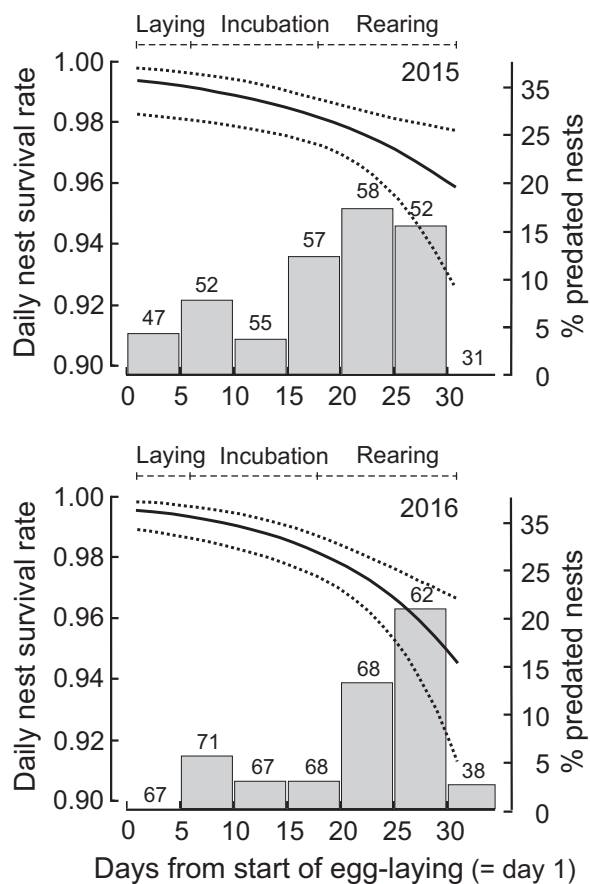
**Figure 3.** Changes in the daily nest survival rate and the percentage of predated nests (bars) in relation to nest progression in 2015 and 2016. Means (solid line) and 95% confidence intervals (dashed line) of daily nest survival estimates are shown. The total number of all nests (*n*) is given above the bars.

*et al.* 2018). This indicates that rodent predation of nests is unlikely to be a main driver of the inverse fluctuations in the numbers of these animals and breeding Wood Warblers, as reported from BNP and other populations across Europe (Wesołowski *et al.* 2009, Szymkowiak & Kuczyński 2015, Pasinelli *et al.* 2016, A. Grendelmeier unpubl. data). Nevertheless, abundant small rodents on the forest floor might have a pivotal indirect effect on the settlement decisions of breeding Wood Warblers; by attracting rodent-hunting specialists such as foxes or martens that hunt prey on the ground where the birds' nests are also situated, small rodents could be responsible for increased nest losses of birds in years of rodent outbreaks (Jędrzejewska & Jędrzejewski 1998, Wesołowski *et al.* 2009, Grendelmeier *et al.*

2018). If this hypothesis is correct, Wood Warblers could use rodent activity on the forest floor as an indicator of the predation risk from carnivores, which are particularly effective in predating the nests, to reduce the likelihood of nest failure by avoiding settling in areas of high rodent abundance (Wesołowski *et al.* 2009, Grendelmeier *et al.* 2018). Further investigations are necessary to explore these relationships fully.

The actual and potential predators recorded at Wood Warbler nests in BNP included birds and mammals, but predatory attacks were carried out almost exclusively by mammals, and mainly at night. Our results were consistent with previous observations of the same or other mammalian species predating bird nests, typically at night (e.g. Picman & Schriml 1994, Pietz & Granfors 2000, Schaefer 2004, Teunissen *et al.* 2008, Weidinger 2010, Meisner *et al.* 2014). These results supported the expectation of predominantly nocturnal nest predation by species that use mainly sound or olfaction for prey detection. Additionally, as nocturnal attacks by carnivores in BNP happened more often than expected from the diel activity of these predators passing by the nests, carnivores seemed to be particularly efficient at finding nests after nightfall. This might be due to increased hunting activity of these predators at night (Wereszczuk & Zalewski 2015, Mason *et al.* 2018), when small rodents were also more active on the forest floor (Fig. 1). However, Wood Warbler chicks might also create sounds by moving around in the nest, which could attract hunting carnivores. During the day, parent Wood Warblers outside the nest can alert their chicks to be quiet by producing alarm calls in reaction to a nearby predator (Cramp 1992, Maziarz *et al.* 2018), but this is unlikely at night when adults are roosting.

The results for all Wood Warbler nests showed that nest survival decreased from the egg stage to the end of the nestling period, mainly due to predation and in line with previous studies (Wesołowski 1985, Wesołowski & Maziarz 2009, Mallord *et al.* 2012, Grendelmeier *et al.* 2015). A higher rate of nest predation in the nestling period is commonly attributed to increased parental activity at the nest as the chicks develop (Martin *et al.* 2000, Zanette *et al.* 2011). However, this cannot explain the observed pattern in the current study, as most attacks occurred at night when parental feeding ceases. Instead, increased predator detection of nests containing older and louder chicks could underlie this result.

In contrast to previous Wood Warbler studies (Wesołowski 1985, Wesołowski & Maziarz 2009, Mallord *et al.* 2012, Grendelmeier *et al.* 2015), nest survival varied little with the timing of breeding, between years or habitats in BNP, suggesting low temporal and spatial variation in the predation pressure on ground-nesting Wood Warblers within the breeding season as well as in the habitats and years studied.

Successful nesting due to predator avoidance can result from several scenarios, such as a potential predator not occurring at a nest, failing to detect the nest when in the vicinity, or detecting a nest but not attacking it, perhaps through distraction or disinterest. Additionally, a predator attack may be ineffective due to the defences or escape of birds in the nest. In this study, potential predators did not occur at 27% of 85 camera-monitored nests and they were recorded passing by almost half of nests. In at least one-third of the occasions when a potential predator was foraging near a camera-monitored nest, it probably passed it by due to a failure to recognize or detect a nest (Schmidt 1999). On another six occasions, when predators inspected nests without attacking them, Wood Warblers might have deterred or repelled predators by producing 'hissing' calls (such defensive behaviour has been found in several songbirds, including Wood Warblers; Cramp 1992, Zub *et al.* 2017). These defensive behaviours and 'near misses' could be important, as if all of the situations when a predator was recorded near a nest had ended with a successful attack, the proportion of depredated nests would be 71%. In addition, had at least one Wood Warbler nestling not escaped from each of six other nests that were attacked, complete losses to predation at camera-monitored nests would have been 78% instead of the 35% recorded. Thus, the breeding success of birds could be enhanced by their various anti-predator strategies, although it might also depend on the random probability of potential predators appearing at nests while actively hunting and detecting nests.

As expected from the predominance of predation by mammals (94% of attacks where the predator species could be identified were by mammals), we found no relationship between nest survival and nest visibility, as also shown in a previous study of Wood Warblers in BNP (Wesołowski 1985). As such, it seems that hiding a nest would give Wood Warblers little defence against mammals, although it could impair nest detection by visually oriented predators. However, this pattern contrasted with findings from Switzerland and the UK, where predation by birds was more common (Grendelmeier *et al.* 2015, Bellamy *et al.* 2018). In Switzerland and Germany, mammals accounted for respectively 63% and 58% of predation events, respectively (Grendelmeier *et al.* 2015, P. Stelbrink unpubl. data). In the UK, birds have been recorded as being responsible for most predation events (e.g. 93% in Wales, Mallord *et al.* 2012; 66–68% in Devon, Bellamy *et al.* 2018), although it constituted only 41% of all predation records in the New Forest, UK (Bellamy *et al.* 2018). The disparities in communities of Wood Warbler nest predators between regions could be a legacy of human activity influencing geographical distribution, local abundance and/or behaviour of predator species, compounded by modification of habitat structure. Several mammals found attacking Wood Warbler nests in BNP are absent or scarce in the UK due to human activity (IUCN 2017), although most species recorded in BNP are also relatively common in Switzerland (IUCN 2017). Almost all nest predators detected in Western Europe are found in BNP (Tomiałojć *et al.* 1984, Wesołowski 1985, Mallord *et al.* 2012, Grendelmeier *et al.* 2015, Maziarz *et al.* 2018), but only some of them were recorded attacking Wood Warbler nests in BNP. A particularly striking difference concerned the Eurasian Jay *Garrulus glandarius*, which was a major nest predator of Wood Warblers in Western Europe (Mallord *et al.* 2012, Grendelmeier *et al.* 2015, Bellamy *et al.* 2018, Maziarz *et al.* 2018, P. Stelbrink unpubl. data) but was unrecorded attacking nests in BNP despite being common in the forest (Tomiałojć *et al.* 1984, Wesołowski *et al.* 2015). This differing impact of Jays on Wood Warblers in the near-primaeval vs. anthropogenically transformed habitats could be due to the relative abundance of predators and prey and/or to differences in habitat structure which may influence predator behaviour (e.g. Andrén *et al.* 1985, Andrén 1992).

Predation has long been recognized as an important selective pressure shaping the evolution of reproductive behaviour in birds and other animals. However, many studies of predator–prey interactions are carried out in habitats heavily affected by humans. Our study shows that the community of species predating Wood Warbler nests can differ between primaeval and anthropogenically modified forests, which might affect the patterns of nest predation. Whereas some defences, such as nest

concealment, may be relatively ineffective against nocturnal carnivores, they may be crucial in avoidance of visually oriented nest predators. Thus, studies conducted across species' ranges and in different habitats are needed to increase our understanding of how selection, imposed by predators, acts on potential prey species in circumstances of different anthropogenic pressures.

## REFERENCES

**Andrén, H.** 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* **73**: 794–804.

**Andrén, H., Angelstam, P., Lindström, E. & Widén, P.** 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. *Oikos* **45**: 273–277.

**Bartoń, K.** 2018. *MuMIn: multi-model inference*. R package version 1.40.4. https://CRAN.R-project.org/package=MuMIn

**Bates, D., Mächler, M., Bolker, B. & Walker, S.** 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**: 1–48.

**Bellamy, P.E., Burgess, M.D., Mallord, J.W., Cristinacce, A., Orsman, C.J., Davis, T., Grice, P.V. & Charman, E.C.** 2018. Nest predation and the influence of habitat structure on nest predation of Wood Warbler *Phylloscopus sibilatrix*, a ground-nesting forest passerine. *J. Ornithol.* **159**: 493–506.

**Benson, T.J., Brown, J.D. & Bednarz, J.C.** 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. *J. Anim. Ecol.* **79**: 225–234.

**Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Multimodel Inference. A Practical Information-theoretic Approach*, 2nd edn. New York: Springer-Verlag.

**Cramp, S. (ed.)** 1992. *The Birds of the Western Palearctic*, Vol. VI. Oxford: Oxford University Press.

**Edmunds, M.** 1974. *Defence in Animals*. New York: Longman.

**Gelman, A. & Su, Y.-S.** 2016. *arm: Data analysis using regression and multilevel/hierarchical models. R package version 1.9-1.* https://CRAN.R-project.org/package=arm (accessed 5 October 2017).

**Goszczyński, J.** 2002. Home ranges in red fox: territoriality diminishes with increasing area. *Acta Theriol.* **47**: 103–114.

**Grant, T.A., Shaffer, T.L., Madden, E.M. & Pietz, P.J.** 2005. Time-specific variation in passerine nest survival: new insights into old questions. *Auk* **122**: 661–672.

**Grendelmeier, A., Arlettaz, R., Gerber, M. & Pasinelli, G.** 2015. Reproductive performance of a declining forest passerine in relation to environmental and social factors: implications for species conservation. *PLoS ONE* **10**: e0130954.

**Grendelmeier, A., Arlettaz, R. & Pasinelli, G.** 2018. Numerical response of mammalian carnivores to rodents affects bird reproduction in temperate forests: a case of apparent competition? *Ecology and Evolution* **8**: 11596–11608.

**Hazler, K.R.** 2004. Mayfield logistic regression: a practical approach for analysis of nest survival. *Auk* **121**: 707–716.

**Holway, D.A.** 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. *Condor* **93**: 575–581.

**IUCN** 2017. *The IUCN red list of threatened species.* Version 2017-1. http://www.iucnredlist.org (accessed 24 July 2017).

**Jędrzejewska, B. & Jędrzejewski, W.** 1998. *Predation in Vertebrate Communities. The Białowieża Primaeval Forest as a Case Study.* Berlin: Springer Verlag.

**Lima, S.L.** 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biol. Rev.* **84**: 485–513.

**Lima, S.L. & Dill, L.M.** 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.

**Mallord, J.W., Orsman, C.J., Cristinacce, A., Butcher, N. & Stowe, T.J.** 2012. Mortality of Wood Warbler *Phylloscopus sibilatrix* nests in Welsh Oakwoods: predation rates and the identification of nest predators using miniature nest cameras. *Bird Study* **59**: 286–295.

**Martin, T.E., Scott, J. & Menge, C.** 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc. Lond. B* **267**: 2287–2293.

**Mason, L.R., Smart, J. & Drewitt, A.L.** 2018. Tracking day and night provides insights into the relative importance of different wader chick predators. *Ibis* **160**: 71–88.

**Mayfield, H.** 1961. Nesting success calculated from exposure. *Wilson Bull* **73**: 255–261.

**Maziarz, M., Piggott, C. & Burgess, M.** 2018. Predator recognition and differential behavioural responses of adult Wood Warblers *Phylloscopus sibilatrix*. *Acta Ethol.* **21**: 13–20.

**Meisner, K., Sunde, P., Clausen, K.K., Clausen, P., Fælled, C.C. & Hoelgaard, M.** 2014. Foraging ecology and spatial behaviour of the red fox (*Vulpes vulpes*) in a wet grassland ecosystem. *Acta Theriol.* **59**: 377–389.

**Ojanen, M. & Orell, M.** 1978. Method for determining the incubation stage of Pied Flycatcher *Ficedula hypoleuca* eggs. *Ornis Fenn.* **55**: 29–31.

**Pasinelli, G., Grendelmeier, A., Gerber, M. & Arlettaz, R.** 2016. Rodent-avoidance, topography and forest structure shape territory selection of a forest bird. *BMC Ecol.* **16**: 24.

**Picman, J. & Schriml, L.M.** 1994. A camera study of temporal patterns of nest predation in different habitats. *Wilson Bull* **106**: 456–465.

**Pietz, P.J. & Granfors, D.A.** 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *J. Wildl. Manage.* **64**: 71–87.

**R Core Team.** 2018. *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing.

**Reconyx, Inc.** 2013. *Reconyx hyperfireTM high performance cameras.* Instruction manual. http://images.reconyx.com/file/HyperFireManual.pdf (accessed 10 November 2016).

**Reynolds, J.C. & Tapper, S.C.** 1996. Control of mammalian predators in game management and conservation. *Mammal Rev.* **26**: 127–155.

**Schaefer, T.** 2004. Video monitoring of shrub-nests reveals nest predators. *Bird Study* **51**: 170–177.

**Schmidt, K.A.** 1999. Foraging theory as a conceptual framework for studying nest predation. *Oikos* **85**: 151–160.

**Schmidt, K.A., Ostfeld, R.S. & Smyth, K.N.** 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. *Oecologia* **148**: 22–29.

**Shaffer, T.L.** 2004. A unified approach to analyzing nest success. *Auk* **121**: 526–540.

**Szymkowiak, J. & Kuczyński, L.** 2015. Avoiding predators in a fluctuating environment: responses of the Wood Warbler to pulsed resources. *Behav. Ecol.* **26**: 601–608.

**Teunissen, W., Schekkerman, H., Willems, F. & Majoor, F.** 2008. Identifying predators of eggs and chicks of Lapwing *Vanellus vanellus* and Black-tailed Godwit *Limosa limosa* in the Netherlands and the importance of predation on wader reproductive output. *Ibis* **150**(Suppl 1): 74–85.

**Thompson, F.R.** 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* **149**(Suppl 2): 98–109.

**Thompson, F.R. & Burhans, D.E.** 2003. Predation of songbird nests differs by predator and between field and forest habitats. *J. Wildl. Manage.* **67**: 408–416.

**Tomialojc, T.** 1991. Characteristics of old growth in the Bialowieza Forest, Poland. *Nat. Areas J.* **11**: 7–18.

**Tomiałojć, L. & Wesołowski, T.** 2004. Diversity of the Białowieża Forest avifauna in space and time. *J. Ornithol.* **145**: 81–92.

**Tomiałojć, L., Wesołowski, T. & Walankiewicz, W.** 1984. Breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland). *Acta Ornithol.* **20**: 241–310.

**Weidinger, K.** 2010. Foraging behaviour of nest predators at open-cup nests of woodland passerines. *J. Ornithol.* **151**: 729–735.

**Wereszczuk, A. & Zalewski, A.** 2015. Spatial niche segregation of sympatric Stone Marten and Pine Marten – avoidance of competition or selection of optimal habitat? *PLoS ONE* **10**: e0139852.

**Wesołowski, T.** 1985. The breeding ecology of the Wood Warbler *Phylloscopus sibilatrix* in primaeval forest. *Ornis Scand.* **16**: 49–60.

**Wesołowski, T.** 2007. Primaeval conditions – what can we learn from them? *Ibis* **149**(Suppl. 2): 64–77.

**Wesołowski, T. & Maziarz, M.** 2009. Changes in breeding phenology and performance of Wood Warblers *Phylloscopus sibilatrix* in a primaeval forest: a thirty-year perspective. *Acta Ornithol.* **44**: 69–80.

**Wesołowski, T. & Tomiałojć, L.** 2005. Nest sites, nest depredation, and productivity of avian broods in a primaeval temperate forest: do the generalization hold? *J. Avian Biol.* **36**: 361–367.

**Wesołowski, T., Rowiński, P. & Maziarz, M.** 2009. Wood Warbler *Phylloscopus sibilatrix*: a nomadic insectivore in search of safe breeding grounds? *Bird Study* **56**: 26–33.

**Wesołowski, T., Czeszczewik, D., Hebda, G., Maziarz, M., Mitrus, C. & Rowiński, P.** 2015. 40 years of breeding bird community dynamics in a primaeval temperate forest (Białowieża National Park, Poland). *Acta Ornithol.* **50**: 95–120.

**Zalewski, A., Jedrzejewski, W. & Jedrzejewska, B.** 2004. Mobility and home range use by pine martens (*Martes martes*) in a Polish primaeval forest. *Écoscience* **11**: 113–122.

**Zanette, L.Y., White, A.F., Allen, M.C. & Clinchy, M.** 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* **334**: 1398–1401.

**Zub, K., Czeszczewik, D., Ruczyński, I., Kapusta, A. & Walankiewicz, W.** 2017. Silence is not golden: the hissing calls of tits affect the behaviour of a nest predator. *Behav. Ecol. Sociobiol.* **71**: 79.

## SUPPORTING INFORMATION

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

**Figure S1.** Examples of potential predators passing by and not attacking (a–d) Wood Warbler *Phylloscopus sibilatrix* nests.

**Figure S2.** Examples of predators attacking (a–c) Wood Warbler *Phylloscopus sibilatrix* nests.

**Table S1.** The number of events in which different potential predator species were recorded passing and not attacking Wood Warbler *Phylloscopus sibilatrix* nests in the study plots (M, N, W) or outwith the plots (Outside), in 2015–2016; in 2015 and 2016, respectively, 41 and 44 nests were monitored with cameras: $^c$carnivores, $^r$small rodents, $^o$other.

**Table S2.** The number of events in which different actual predator species were recorded attacking Wood Warbler *Phylloscopus sibilatrix* nests in the study plots (M, N, W) or outwith the plots (Outside), in 2015–2016. The 'unknown' predator was not caught by the camera, but traces such as an empty nest when young should have been present, damaged eggs or dead young indicated predation; in 2015 and 2016, respectively, 41 and 44 nests were monitored with cameras: $^c$carnivores, $^r$small rodents, $^o$other.

**Table S3.** Variables used in modelling daily survival of Wood Warbler *Phylloscopus sibilatrix* nests.