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The Function of White Anthropogenic Material in Jackdaw Nests

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Abstract

Birds invest substantial energy in reproductive activities, from building fat reserves and finding mates to constructing nests and raising young. Nest-building varies significantly across and within species, including incorporating anthropogenic materials like white paper and plastic. This study focuses on jackdaws in Glimmen, the Netherlands, where such materials have been noted in nests. We aimed to investigate the potential functionality of these materials through several hypotheses. Experiments involved manipulating nest boxes with colored feathers and torn paper to test preferences and functions, including antimicrobial properties. Also, we wanted to test the availability hypothesis and the confusion theory, which assumes that jackdaws might be unable to distinguish between anthropogenic and natural nest materials. Additionally, a mesh experiment allowed the active selection of materials and was aimed at optimizing our initial study design. Our orientation analysis explored the effect of orientation-dependent nest box humidity and microclimate on the use of anthropogenic materials, the so-called doormat hypothesis. Furthermore, we aimed to determine an optimal time window for conducting research by performing a time series analysis on different breeding phases. Results indicated jackdaws actively manage nests with colony-specific differences. Jackdaws removed most of the materials offered, and in this study, the experimental setup was not optimized using meshes. However, we suggest further research to confirm this. The orientation analysis partially supported the doormat hypothesis, showing a pattern in material use related to nest box orientation. Lastly, the time series analysis indicated that the period before chick hatching is optimal for conducting experiments concerning white anthropogenic materials in jackdaw nests. Overall, this study provides a framework for future research, suggesting optimal periods for observation and potential improvements in experimental designs. Understanding the functionality of anthropogenic materials in nests can offer broader insights into bird behavior and adaptation.

1 | Introduction

A bird's life revolves mainly around reproductive output, and much energy is invested in this (Sibly et al., 2012; Mainwaring & Hartley, 2013). Throughout the year, a bird tries to build fat reserves for the upcoming breeding season, find a mate, build a nest, incubate their eggs, and finally feed their young until they become fledglings (Gill, 2007). The nest-building stage deviates strongly between bird species; some build complex and elaborate nest structures, while others make simple designs with few materials. Also, within species, even within populations, there is much variation in nest construction, integrity and ornamentation (Deeming et al., 2021; Perez et al., 2023). In several bird species, scientists have noted the presence of white anthropogenic materials in their nests, such as paper and plastic (Briggs & Mainwaring, 2024; Esquivel et al., 2020; Jagiello et al., 2019; Korte, 2023). Jackdaws are one of these bird species, and one long-term study in Glimmen, the Netherlands, has gathered data on these birds for more than 35 years (Verhulst group, 1989-2024). Only in recent years have anthropogenic materials come to their attention. As mentioned, many birds use white foreign objects in their nests, and research on these species might provide information on the potential functionality of anthropogenic materials for jackdaws.

It should be noted that these possible adaptations do come at a cost, namely, a higher risk of entanglement and ingestion (Jagiello et al., 2022; Santos et al., 2021). In the case of this trade-off, the existing functional hypotheses should result in a net benefit. However, incorporating white anthropogenic pieces can be a suboptimal trait, so non-functional hypotheses are also presented in the literature.

Functional hypotheses

Bird nests are frequently considered an example of an extended phenotype (Järvinen & Brommer, 2020). Consequently, numerous functional hypotheses exist regarding the incorporation of white anthropogenic materials into nests, as this behavior is believed to represent an adaptive trait. These hypotheses can be divided into two classes: building materials and signals. The former can take a variety of shapes; namely, the white anthropogenic materials can potentially aid in nest thermoregulation or reinforcement, function as a doormat to prevent moisture damage to the nest or have antimicrobial properties. Close control of the nest microclimate and temperature is essential for chick development and body condition (Mueller et al., 2019). The natural reflectivity of white nest materials can potentially help thermoregulate in both warm and cold environments, as has been shown in a variety of bird species (Corrales-Moya et al., 2021; Deeming et al., 2020; Kull, 1977; Mayer et al., 2019). Anthropogenic materials can increase the structural stability of Great Grey shrikes and tit nests. However, there are species-specific preferences for the type of material (Antczak et al., 2010; Surgey et al., 2012). Furthermore, the nest's microclimate is highly influenced by nest orientation and can cause significant differences in humidity (Carroll et al., 2020; Corimanya et al., 2024). Subsequently, white anthropogenic pieces' usage can be a response to the humidity and function as a 'doormat' to soak up excess water and prevent nest damage. Lastly, in terms of functionality regarding building materials, white foreign objects might convey antimicrobial properties via lowering ectoparasite presence (Hanmer et al., 2017). A high ectoparasite load during chick development can lower fitness and survival, and known adaptations are the inclusion of cigarette buds in the nest lining (Badás et al., 2023; Dudaniec et al., 2006; Suárez-Rodríguez et al., 2013; Suárez-Rodríguez & Garcia, 2017). Also, white-colored feathers are often used as an antimicrobial defense against eggshell bacteria, and white anthropogenic materials might convey the same properties (Peralta-Sánchez et al., 2013; Ruiz-Castellano et al., 2016).

The second class of functional hypotheses constitutes a potential signaling mechanism aimed towards predators, conspecifics or mates. Predation is a significant factor limiting breeding success in jackdaws, and building camouflaged nests could be an adaptive trait (Bailey et al., 2015; Johnsson, 1994). White anthropogenic materials typically do not increase but rather decrease crypticity (Mayer et al., 2009). However, these pieces could confuse egg predators by mimicking the reflection of light onto the water or blurring the body outlines of the bird; so-called disruptive camouflage (Hansell, 1996; Hansell & Overhill, 2000; Korte, 2023; Kull, 1977; Nokelainen & Stevens, 2016). Furthermore, nest materials can function as a signal towards conspecifics, as has been shown in raptors; nest decorations conveyed territorial quality and signaler dominance (Sergio et al., 2011). Lastly, white anthropogenic materials may function as a sexual signal by attracting mates, enhancing parental care or acting as an incubation stimulus (Anderson & Brush, 2016; Coulter, 1980; Jagiello et al., 2022; Sergio et al., 2011).

Non-functional hypotheses

Scientists have also proposed hypotheses where white anthropogenic material in bird nests does not have apparent functionality. Birds might confuse the objects for food or even with their eggs (Conover, 1985). Moreover, human activities have increased anthropogenic material in the environment and decreased natural nest material (Antczak et al., 2010). This could result in birds being more likely to incorporate anthropogenic pieces into their nests since these are more available in their surroundings (Jagiello et al., 2019; Jagiello et al., 2022; Radhamany et al., 2016). Furthermore, foreign objects can be age-related; older black kite and white stork individuals are more prone to using these materials since these would convey individual quality (Jagiello et al., 2018; Jagiello et al., 2022).

Aim of this study

So, while many hypotheses are proposed, and some have already been tested in other bird species, no study has yet focused on unraveling white anthropogenic materials' functionality for jackdaws. Therefore, we provide one of the first reports on the possible hypotheses that might apply to jackdaws, tested in 6 colonies and solo boxes near Glimmen, the Netherlands. In order to do so, we have set up multiple experiments, all of which try to answer the research question: "Why do jackdaws incorporate white anthropogenic materials into their nests?" White anthropogenic materials will be used interchangeably with the term white papers.

This question has high scientific value since, in this day and age, many 'why' questions have already been answered about birds and behavior, and it is therefore rather unique that no scientists yet have been able to unravel the mystery of white foreign objects. Also, since these materials are found in all sorts of bird species globally, understanding their functionality in jackdaws might give insight into a more extensive range of species and their behavior. Furthermore, jackdaws are suitable to study species since they are common in the Netherlands and willing to breed in provided nest boxes. Also, they are monogamous with biparental care, which makes studying reproductive success more accessible (Hahn et al., 2021; Kubitza et al., 2014).

To address the research question, several proposed hypotheses were tested through experimental methods and data analyses. At the outset of this study, the breeding season was already in progress, making it challenging to investigate hypotheses related to sexual and conspecific signaling. Therefore, hypotheses that could be tested were selected based on their plausibility for jackdaws and the availability of necessary materials. Jackdaws in Glimmen breed in closed artificial nest boxes, many of which are equipped with anti-predator fly holes. This setup made it less feasible to test hypotheses related to nest isolation and reinforcement and complicated the examination of anti-predator mechanisms. Ultimately, several hypotheses were tested alongside the optimization of the experimental setup and the determination of the appropriate testing period in the following experiments.

Feather manipulation

Jackdaw nest boxes near Glimmen were experimentally manipulated by supplementing them with colored feathers. This was done to test the color and material preference for feathers when their availability was equal across nest boxes. Given that white feathers possess antimicrobial properties that reduce bacterial load on eggshells, we investigated how jackdaws incorporated these inside their nests to see whether this was similar to the white anthropogenic pieces. We hypothesized that jackdaws would prefer white feathers and preferentially place them in the inner lining of the nest in contact with the eggs. Observations of anthropogenic materials near the fly hole led us to expect differences in the utilization of feathers compared to white paper, suggesting different functionality for the latter. Also, the availability hypothesis would predict that natural nest materials such as feathers would be preferentially kept when made more available than anthropogenic materials, and this is what we expected to see.

Paper manipulation

Jackdaw nest boxes were manipulated by supplementing one torn piece of paper to compare the results to the feather manipulation. We hypothesized that colonies with little white anthropogenic material in their nest boxes would keep the pieces of paper to a greater extent than colonies with high amounts of white paper inside their nest boxes. Colonies with little anthropogenic materials in their nests also had less available in their surroundings. According to the availability hypothesis, they are thus expected to keep the pieces of paper when availability is increased. Also, we expected a clear preference for either feather of paper, which would rule out the confusion hypothesis.

Mesh experiment

To let jackdaws actively select materials and colors, we placed wired meshes with feathers and pieces of torn paper near all the colonies. We hypothesized that allowing active selection under conditions where availability differences were removed would optimize the conditional setups and give more accurate results. We expected a clear preference for color and material and aimed to test the same hypotheses as stated for the feather and paper manipulations.

Nest box entrance orientation analysis

The orientation of all the occupied nest boxes in the 6 colonies near Glimmen was measured and analyzed to determine a pattern in white paper coverage in nest boxes across orientations and test the doormat hypothesis. In the Netherlands, the optimal orientation of a nest box is proposed to be towards the Northeast since prevailing winds often come from the Southwest (Vogelbescherming Nederland, n.d.). We thus hypothesized that nest boxes orientated towards the Southwest would contain the highest percentage of white paper coverage and towards the Northeast the lowest. Furthermore, we expected to see a circular pattern in percentage paper coverage.

Time series analysis

An analysis has been performed to see whether there are differences in the white paper coverage across breeding season stages. Also, we aimed to potentially define an optimal time window to conduct studies regarding the presence of white anthropogenic paper in jackdaw nests. We hypothesized that a substantial decrease would be observed after chicks hatching. Lastly, we expected a clear trend in the percentage of paper coverage over time.

2 | Methods

A graph has been produced with the maximum paper coverage per colony in R studio version 4.2.2. Paper coverage has been retrieved from a dataset with data from the ongoing research on jackdaws in Glimmen (Verhulst group, 1989-2024). All percentages used for further analysis have been determined based on photographs taken of nest boxes. The surface that has been covered with white anthropogenic material has been estimated by visual inspection. Data on lay and hatch date has been obtained from an existing dataset. Lists of the materials that have been used for each experiment can be found in Table 2 Appendix A.

2.1 | Feather manipulation experiment

2.1a | Nest box selection

43 jackdaw nest boxes out of the 6 colonies near Glimmen have been manipulated in this experiment. Further selection resulted in a sample size of 41 nest boxes and was based on the following two conditions: the nests needed to be actively occupied by jackdaws, and the couple was just before the start of or in the egg-laying phase of the breeding season, see Figure 1. The egg-laying phase was determined by visiting the nest every third day. The phase started when the first jackdaw egg was observed, and when the same number of eggs was found twice in a row, the egg-laying phase was considered to be over, and incubation started.

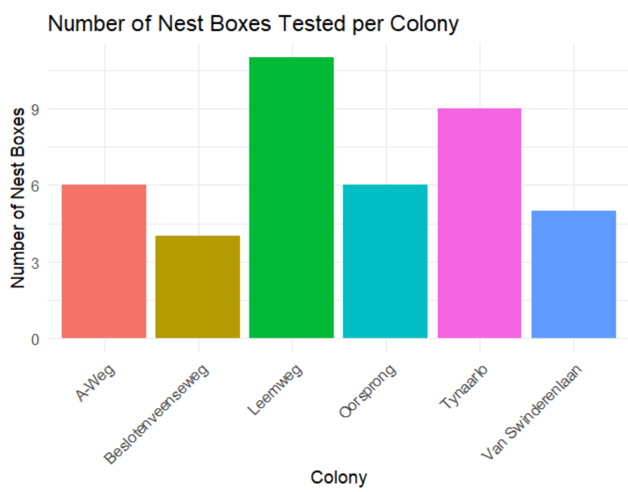

Figure 1: Bar plot of the total number of nest boxes on which feather manipulations were performed, grouped by individual colonies.

2.1b | Procedure

Each of the 41 nests was manipulated by supplementing two feathers near the nest's opening. The combination of similar-sized feathers was randomly selected with one white feather with a colored feather (light pink, light blue, orange, yellow or green) or a light-colored feather (light pink and light blue) with a colored feather. Also, two white feathers of different sizes were added to one nest. Feather sizes were manipulated by the use of scissors and they were placed parallel to each other, with the feather pins facing the same direction. The placement of the white feather altered randomly between the closest to the nest box entrance and the farthest away from the nest box entrance. After each manipulation, photographs were taken to show the pre-experiment conditions. 3 cameras were set up for two hours to examine the activity inside the nest of the jackdaws upon entering the nest after manipulation. After three days, all 41 nests were checked for the presence of feathers; when this was the case, photographs were taken.

2.1c | Data analysis

No statistical analysis has been performed on the obtained data; rather, a description of the observations has been made since the statistical power was too low to be informative.

2.2 | Paper manipulation experiment

2.2a | Nest box selection

For this experiment, the same 41 nest boxes as in experiment 2.1 have been selected using the corresponding two conditions (see Section 2.1a).

2.2b | Procedure

Each nest box has been manipulated by adding one torn piece of white 300-gram paper of around 5 x 5 cm near the entrance, except for one nest box where two pieces of paper were added. 3 nest boxes were manipulated with pieces of paper marked with the corresponding nest box number, and observations were done up to two weeks after the manipulation to check for marked pieces of 300-gram paper. Photographs were taken after each manipulation, and 3 cameras were set up inside the nests to film for two hours to examine jackdaw activity immediately after the manipulation. All 41 nests were checked after two days for the presence of white 300-gram paper, and photographs were taken when this was the case.

2.2c | Data analysis

No statistical analysis has been performed on the obtained data; rather, since the statistical power was too low to be informative, the observations have been described.

2.3 | Mesh experiment

2.3a | Mesh placement selection

A wired mesh has been placed in every of the 6 colonies near Glimmen. This study adapted the method described by Ruiz-Castellano et al. (2017) where plastic meshes were used to offer nest materials to spotless starlings. We modified this approach by utilizing different mesh sizes and wired meshes to provide a more durable option. The meshes were placed away from public roads or walking trails to limit interference with the experiment by others. Furthermore, it was ensured that the mesh was visible for jackdaws by placing them near open vegetation and not further away than 5 meters from the colony.

2.3b | Procedure

6 meshes of 50 cm by ~85 cm were made with mesh sizes of 2.5 cm, one for every colony near Glimmen. At one half of the mesh, different colored feathers (white, light pink, light blue, green,

orange and yellow) were placed, and at the other, torn pieces of 300-gram paper of around 5 x 5 cm were placed. Meshes were secured using ground cover pegs, and photographs were taken to show the pre-experiment conditions. A random number of feathers and pieces of paper were put in each mesh, and after three days, the meshes were observed, and nest boxes were checked for the presence of feathers or 300-gram paper inside the nests. 2 cameras were placed to film for two hours to see whether the jackdaws were near the mesh.

2.3c | Data analysis

No statistical analysis has been performed on the obtained data since no jackdaw activity has been observed.

2.4 | Nest box entrance orientation analysis

2.4a | Nest box selection

84 nest boxes have been selected to measure the orientation of their nest box entrance (N, NE, E, SE, S, SW, W or NW) from all 6 colonies near Glimmen and several solo nest boxes outside these colonies. The selection was based on the following two conditions: the nest boxes have been actively occupied by jackdaws during the observational period from the 27th of March until the 12th of May 2024, and during this period, there has been at least one observation of the percentage of white paper coverage in the nest box.

2.4b | Procedure

The orientation of the nest box entrance of the 84 nest boxes was acquired using a compass (N, NE, E, SE, S, SW, W or NW). This was done by facing 180 degrees away from the nest box entrance and observing the direction in which the nest box entrance is orientated. Furthermore, from the 27th of March until the 12th of May 2024, the maximum observed percentage of white paper coverage was obtained from a dataset containing observational data from this period. Obtained data has first been converted to degrees and radials.

2.4c | Data analysis

An analysis in R studio version 4.2.2 has been performed to test for possible correlations between nest box entrance orientation and percentage white paper coverage in jackdaw nest boxes. Nest box entrance orientation is a circular covariate, and percentage white paper coverage is a linear covariate. Therefore, a linear regression model has been fitted with the sine and cosine of the orientation to account for its circularity. Furthermore, to test for the influence of Tynaarlo on the paper coverage per orientation, a second linear regression model was fitted with a dummy variable (1 = Tynaarlo 0 = other colonies) and also included the interaction of Tynaarlo with the cosine and sine of the orientation.

2.5 | Time series analysis

2.5a | Nest box selection

For the time series analysis of the lay date, 19 nest boxes were selected in the colony of Tynaarlo based on the condition that a lay date would be recorded from the 27th of March until the 12th of May. Similarly, for the time series analysis of the hatch date, nest boxes in Tynaarlo were selected when, in the period mentioned above, a hatch date was recorded; this resulted in a total of 15 nest boxes. Lastly, for the time series analysis of breeding season phases, nest boxes in Tynaarlo were selected when, in the named period, at least the lay date was recorded. Thus, a total of 19 nest boxes were selected.

2.5b | Procedure

For the time series analysis of the lay date, a dataset containing observations of the percentage of coverage of white paper in nest boxes of jackdaws from the 27th of March until the 12th of May has been transformed to a time scale where 0 represents the lay date. The days before or after the lay date have been adjusted to a negative or positive number, respectively. The same has been done for the time series analysis of the hatch data, where 0 represents the hatch date. Lastly, based on the recorded lay and hatch date, the white paper coverage observations have been divided into 4 breeding season phases. The pre-egg-laying phase is the period before the recorded lay date, and the egg-laying phase (the lay date plus the total clutch size since jackdaws typically lay one egg each day after the first egg) form the first phase. The incubation phase begins after the egg-laying phase and stops before hatching; the hatching phase corresponds to the hatching date, the 5-day phase indicates the fifth day after hatching (where hatching is day 1) and together, the 10-day phase (the tenth day after hatching) form the fourth phase. The average of all observations within a particular phase has been utilized for further analysis.

2.5c | Analysis

An analysis in R studio version 4.2.2 has been performed to test the effect of various factors on the percentage of white paper coverage inside the jackdaws nest boxes. An arcsine square root transformation has been applied for all analyses (lay date time scale, hatch date time scale and breeding phases). This is done since the assumption that the variance is independent of the mean (the homoscedasticity assumption) does not hold for proportions (in this case, percentages). Furthermore, data points are not independent because data from the same nest boxes but from different time points or phases have been obtained. For this reason, mixed effect models have been fitted where the nest boxes are accounted for as the random effect.
For the lay date-time scale analysis, a dummy variable has been added to test for the effect of the presence of chicks (0 = not hatched, 1= at least one young has hatched). Also, the lay date has been taken into account to see whether the day in April when jackdaws started laying their first egg influences the percentage of white coverage. The effect of time on paper coverage and the interaction between time and the presence of chicks has been added to the mixed effect model. A second model has been fitted, where only the data points after the hatching of chicks

have been utilized, to test for a significant increase or decrease of paper coverage after the young are present.

A mixed-effect model for the hatch date-time scale analysis has been fitted to test for the effect of the presence of chicks, time, and their interaction. A second model has also been fitted, similarly to the lay data time scale analysis, where only the observations with chicks present have been selected to test for a significant increase or decrease of paper coverage.

Lastly, an analysis has been performed to test whether there is a significant difference between any of the 4 breeding season phases in their percentage of paper coverage inside the jackdaw's nests. A mixed model was fitted where the ordering of the phases was taken into account, and its effect on paper coverage was tested.

In the case of significant effects and corresponding p-values, the appropriate post hoc tests have been performed, and model assumptions have been checked.

3 | Results

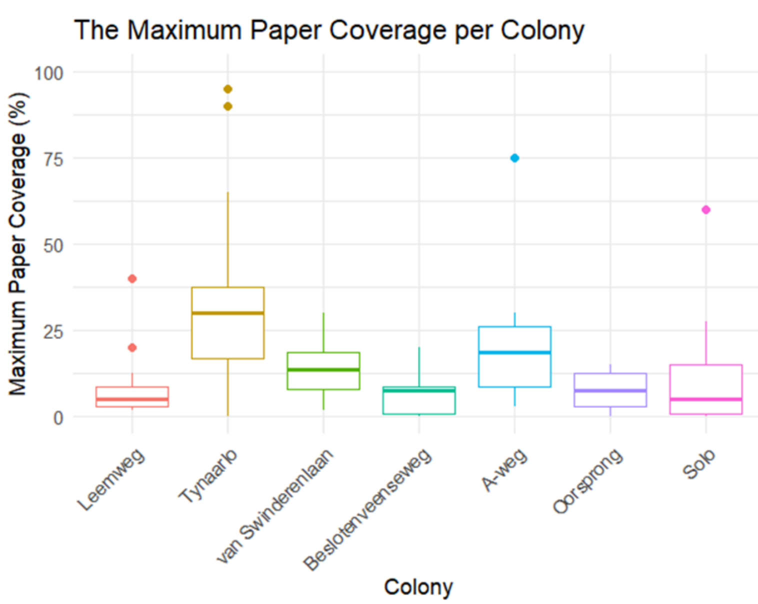

Figure 2: Box plot of the maximum observed paper coverage in nest boxes grouped by colony. Solo boxes have been grouped together.

In Figure 2, it is shown that Tynaarlo has the highest maximum percentage coverage of all colonies and solo boxes. Leemweg and Beslotenveenseweg have the lowest maximum paper coverage.

3.1 | Feather manipulation experiment

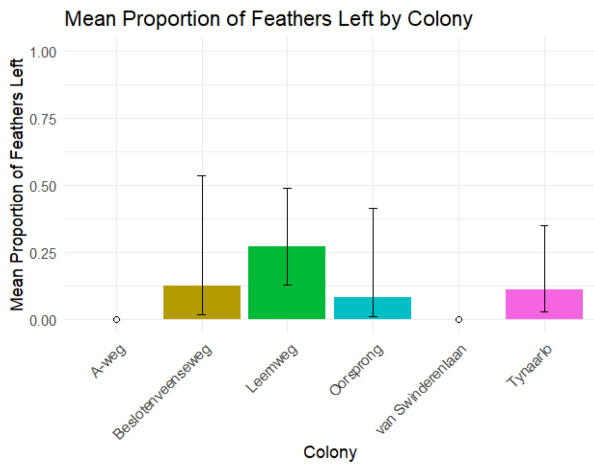

Figure 3: Bar plot of the mean number of feathers left after three days as a proportion of the number of manually supplemented feathers, grouped by individual colonies. Black lines indicate the 95% confidence interval. Circles show that no confidence interval could be calculated, which occurred only when all data points for the respective colony were 0.

In Figure 3, the mean proportion of feathers remaining in the nests is shown, grouped by colony and the confidence intervals. In total, 10 out of 82 feathers were found back after three days. Leemweg showed the highest mean proportion of feathers left (prop. = 0.27), around twice as high as the three other colonies where feathers were found back. Furthermore, in the A-weg and van Swinderenlaan, no feathers remained in the nests, so no confidence interval was computed. The colors of the feathers that remained were white (n = 4), yellow (n = 3), and orange (n= 3) and 8 out of 10 feathers were found in the outer lining; the other two were placed in the inner lining of the nest.
The 3 cameras set up were analyzed, and video footage was obtained. In two of the videos, copulation was observed after the jackdaws returned to their nest boxes and inspected the feathers. Furthermore, in one nest box, no jackdaws returned within the two-hour time frame. Another couple removed both feathers, and the other initially kept them, but after three days, both were removed.

3.2 | Paper manipulation experiment

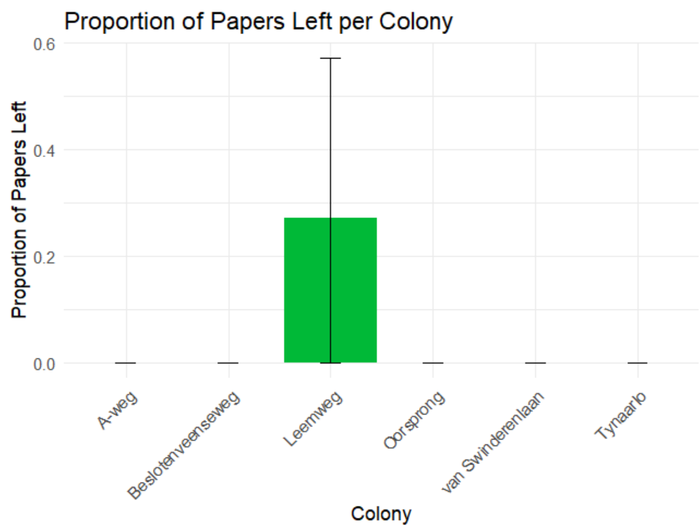

Figure 4: Bar plot of the number of pieces of paper left after two days as a proportion of the number of manually supplemented pieces, grouped by individual colonies. Black line indicates the 95% confidence interval.

Figure 5: Photo showing the inside of nest box 906 with a marked 300-gram paper originally placed in nest box 904, taken on 02-05-2024. The nest box entrance is located in the bottom right corner.

3 out of 41 pieces of 300-gram paper were left after two days of manipulation. Leemweg was the only colony where papers were found back in three of the nests, as in the other colonies, all pieces of paper were removed, see Figure 4. After one week of manipulation, one of the marked pieces of 300-gram paper was found in another nest box within the same colony, A-weg, see Figure 5. Furthermore, the video footage did not show any jackdaw couples removing the pieces of paper provided or relocating them within the nest within the two-hour time frame.

3.3 | Mesh experiment

The video footage obtained of the first two hours after the meshes had been placed showed no activity. Also, after three days, no feathers or pieces of 300-gram paper were found inside any of the jackdaw nests of the 6 colonies near Glimmen. The meshes were still present and in the same location.

3.4 | Nest box entrance orientation analysis

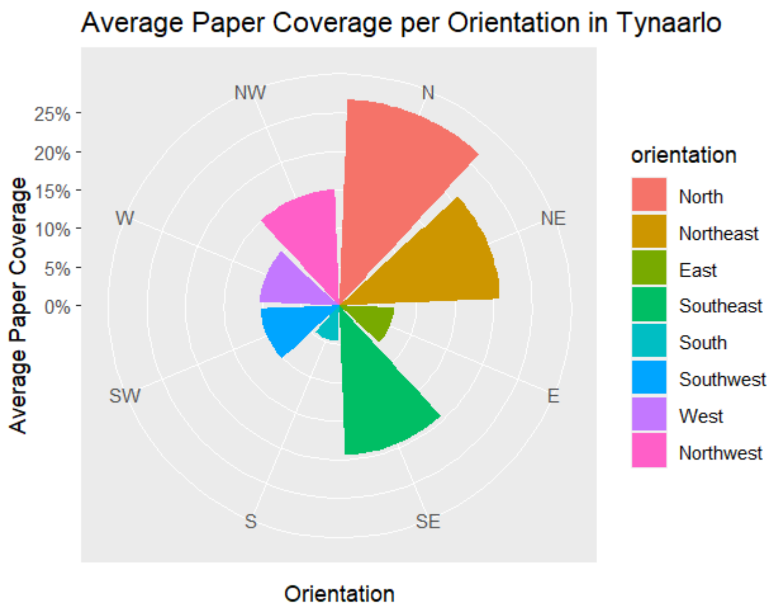

Figure 6: Circle diagram of the mean paper coverage in the colony of Tynaarlo, grouped by orientation. Each orientation constitutes an angle of 45º.

The average paper coverage per orientation has been computed and visualized in Figure 6. Nest boxes with their nest box entrance orientated towards the North had the highest percentage of average paper coverage, and nest boxes orientated towards the South had the lowest. The linear regression model that had been fit was statistically significant (F = 4.71, df = 2, p = 0.012, R^2 = 11.16%). The cosine of the orientation significantly affected paper coverage (p = 0.0043), the sine of the orientation non-significantly affected this (p = 0.60), see Table 3a Appendix B.

The second linear regression model that tested the effect of the colony of Tynaarlo and its interaction with the cosine and sine of the orientation on the paper coverage also was statistically significant (F = 8.289, df = 5, p = 3.2 * 10^-06, R^2 = 36.53%). While not significant under the significance threshold of p= 0.05, a trend has been found where Tynaarlo has a higher percentage of paper coverage, estimated at 20.1% higher, than other colonies (p = 0.13), see Table 3b Appendix B. In this model, the cosine and sine of the orientation no longer significantly affect the paper coverage (p = 0.47 and p = 0.55, respectively). The model estimated the interaction of Tynaarlo with the cosine of the orientation to increase the paper coverage with 6.6%, however, not significantly (p = 0.61).

3.5 | Time series analysis

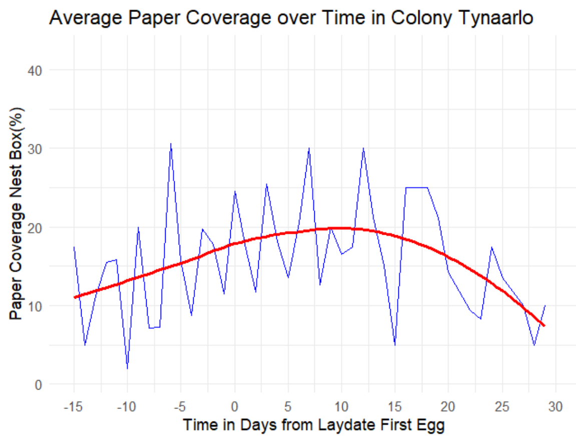

Figure 7a: The mean paper coverage in the colony of Tynaarlo over time with the lay date of the first egg as t= 0. The red line represents the trend and the blue line represents the mean paper coverage for each day.

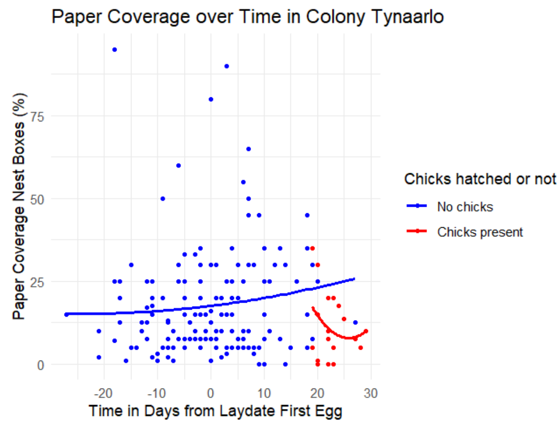

Figure 7b: The paper coverage in the colony of Tynaarlo over time with the lay date of the first egg as t= 0, grouped by the presence or absence of chicks. Dots represent individual data points and the lines represent trends. Dots correspond to nest boxes sampled multiple times.

In Figure 7a, the average paper coverage over time in the colony of Tynaarlo is shown, where 0 represents the lay date. A clear quadratic relationship is visible with a gradual increase in paper coverage and a decrease around t = 20, which is around the hatch date of the first chicks.
A mixed effect model with the nest boxes as the random effect has been fit to test how the paper coverage is affected by the covariate's time, the presence of chicks, its interaction and the lay date. An intraclass correlation coefficient (ICC) of 0.3478 was computed, meaning that 34.8% of the observed variation could be attributed to variation between nest boxes. Furthermore, none of the covariates significantly affected the paper's coverage, see Table 4a Appendix C. Figure 7b shows a negative trend in the paper coverage after the chicks have hatched. A second mixed-effect model, which included a subset of only hatch data, showed that when chicks are present, the paper coverage showed a marginally significant decrease over time ($p = 0.061$), see Table 4b Appendix C.

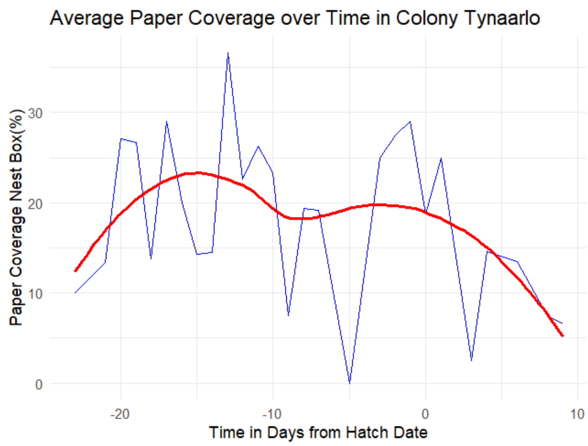

Figure 8a: The mean paper coverage in the colony of Tynaarlo over time with the hatch date of the first chick as t= 0. The red line represents the trend and the blue line represents the mean paper coverage for each day.

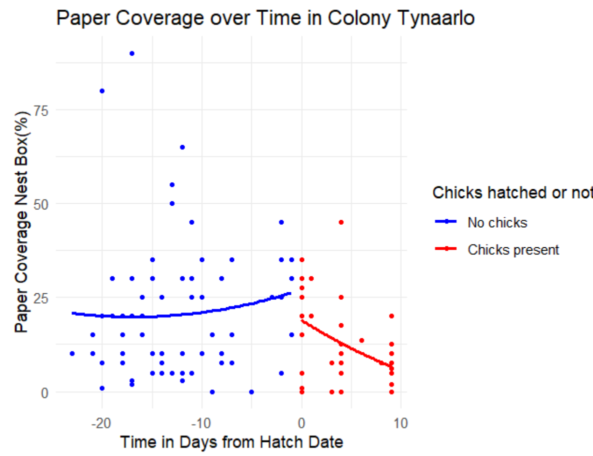

Figure 8b: The paper coverage in the colony of Tynaarlo over time with the hatch date of the first chick as t= 0, grouped by the presence or absence of chicks. Dots represent individual data points and the lines represent trends. Multiple dots correspond to the same nest box.

In Figure 8a, the average paper coverage over time in the colony of Tynaarlo is shown, where 0 represents the hatch date. Here, a clear quadratic relationship can also be observed with an initial increase in paper coverage and a sharp decrease after the hatch date, when the chicks are present.

A mixed effect model with the nest boxes as the random effect has been fit to test how the paper coverage is affected by the covariates time, the presence of chicks and its interaction. An ICC of 0.3478 was computed, similar to the ICC of the lay date model. While there were no significant effects of the covariates found on the paper coverage, there was a negative trend found in the interaction of time with the presence of chicks ($p = 0.083$), see Table 5a Appendix C. In Figure 8b, again, a clear decrease in paper coverage can be observed after the chicks have hatched. A mixed-effect model that only included data after the hatch date found that the paper coverage significantly decreased over time when chicks were present ($p = 0.024$), see Table 5b Appendix C.

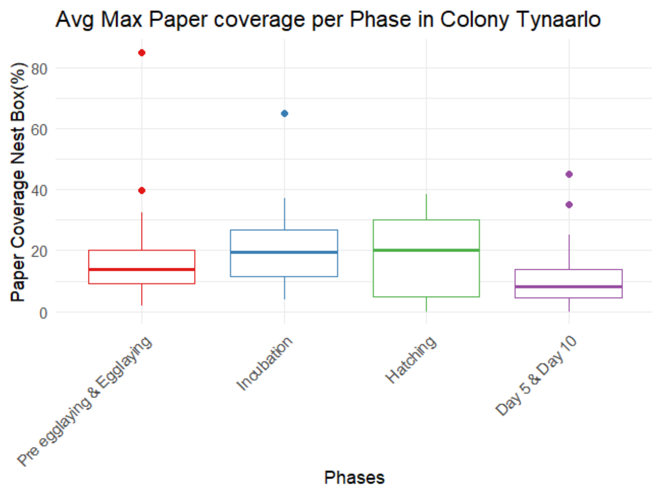

Figure 9: Boxplot of the mean of the maximum paper coverage in colony Tynaarlo, grouped by phase.

In Figure 9, the paper coverage in the colony of Tynaarlo has been shown across 4 phases. The highest coverages were observed in the incubation and hatching phases, and the lowest was observed after the chicks had hatched (measured at five days old and ten days old). A mixed-effect model with the nest boxes as the random effect has tested how the covariate phases affect the paper coverage. A significant effect of phase on paper coverage was found using a type II ANOVA with the Kenward-Roger method (F, df=3, $p = 0.045$). A post hoc analysis using the Tukey HSD method showed that the paper coverage in the incubation phase differed significantly from the day 5 & day 10 phases ($p = 0.033$), see Table 6 Appendix C.

4 | Discussion

In this study, our primary objective was to investigate the potential functionality of white anthropogenic materials in jackdaw nests. To do this, we reviewed multiple hypotheses from existing literature (Table 1), some of which we then tested through a series of experiments and analyses. By focusing on these specific materials and their potential roles in nest construction, we aimed to provide new insights into the behavior of jackdaws and suggest future research directions in this field.

We tried to test the availability, antimicrobial and confusion hypothesis with our feather and paper manipulation experiment. We expected an explicit material and color preference and differences in utilization to rule out the confusion hypothesis. Also, we expected a preference for white feathers since these are known to convey antimicrobial properties (Peralta-Sánchez et al., 2013; Ruiz-Castellano et al., 2016). A different utilization of these feathers compared to the 300-gram paper would imply different functionality for the white anthropogenic pieces in the nest. Furthermore, by increasing the availability, we expected jackdaws to preferentially keep the materials we offered. Results were inclusive, and most feathers and 300-gram papers were removed from the nests. The kept feathers and papers resulted in a sample size unsuitable for further analysis since the statistical power would be too low to be informative. This led to neither of the three examined hypotheses being rejected or confirmed based on these experiments.

Our results did reveal some other interesting observations. Namely, we found strong evidence that jackdaws actively manage their nests and that colony-dependent and couple-specific differences exist in this management. Five of the nine jackdaw couples that kept material offered in at least one of the two experiments were situated in the colony of the Leemweg. Two couples even kept both the offered feathers and the piece of 300-gram paper. This could be related to experience since this is known to influence nest material choice in birds (Bailey et al., 2014; Muth & Healy, 2011). However, this could not be confirmed based on the available data on the specific jackdaw couples, and local individual differences might explain the observed pattern (Mennerat et al., 2009).

Ultimately, we hypothesized that the experimental setup used might be suboptimal in testing for general trends and preferences. Nest box manipulation seemed to test individual jackdaw differences in their willingness to accept foreign objects and their level of active management. Similar results were found in a study on the Kentish plover; researchers stated that all material added to the nest was removed by the majority of the birds, irrespective of type or coloration (Gómez et al., 2019). Therefore, we designed a grid experiment to optimize our research setup and have more accurate and conclusive results, which has been successful in other studies (Ruiz-Castellano et al., 2017). The aim was similar to the feather and paper manipulation experiment: testing the availability, antimicrobial and confusion hypothesis. Unfortunately, this experiment did not yield informative results since no material had been taken from the six grids, and no jackdaw activity near the grids had been observed. We hypothesized that this can be attributed to the period in which this experiment has been conducted. Namely, the incubation phase was nearing its end for most nest boxes, and chicks began to hatch. Our time series analysis identified a negative trend in paper coverage after the hatch date across all colonies. This implies that jackdaws were no longer gathering nest material but removed this. Based on the previous research utilizing grids for testing material preferences (Ruiz-Castellano et al., 2017), this research setup can be effective if placed during the nest building stage. That is what we suggest for future research. Also, a second option is to replace anthropogenic material from one nest box to another to optimize the experimental setup since jackdaws have already accepted and actively chosen this material.

For the nest box orientation analysis, we aimed to test the doormat hypothesis. We hypothesized that nest box entrances oriented towards the Southwest would contain the highest percentage of white paper coverage and the lowest would be found in those nest boxes oriented towards the Northeast. Results indicated that this was not the case; North-oriented nest boxes contained the most white paper, and thus, our main hypothesis was rejected. However, we also expected to see a circular pattern concerning white anthropogenic coverage per orientation, and this is what was found. Namely, the cosine of the orientation significantly affected the paper coverage and a pattern was observed despite this being different from the initial expected pattern. This could possibly be explained by the weather variability during the study period in terms of precipitation and wind direction. In Figure 10, it is shown that our prior assumption stating that wind in the Netherlands comes primarily from the Southwest does not hold (Weer

Archief Nederland, n.d.). Out of the fifteen measurements, the wind came from the Southwest only twice. Also, precipitation was only present on certain days, which can have influenced the humidity in the nest boxes and, subsequently, the paper coverage. However, this does not explain the high paper coverage observed in nest boxes oriented towards the North in our analysis. Therefore, we did further research and found that the majority of the nest boxes in the colony of Tynaarlo have been oriented towards the North, see Figure 11. This colony has the highest observed percentages of white paper coverage and might have influenced the results. Further analyses confirmed a marginally significant trend in the effect of Tynaarlo on the paper coverage per orientation. Therefore, we recommend further testing the doormat hypothesis to see if the results can be replicated when accounting for colony-dependent influences.

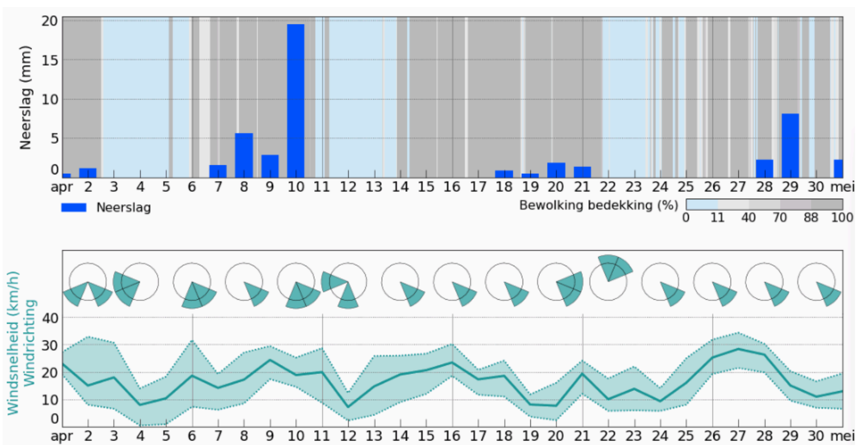

Figure 10: Precipitation (=neerslag), cloud coverage (=bewolking bedekking), wind speed (=windsnelheid) and wind direction (=windrichting) during April 2024 in the Netherlands. Figure obtained from Weer Archief Nederland.

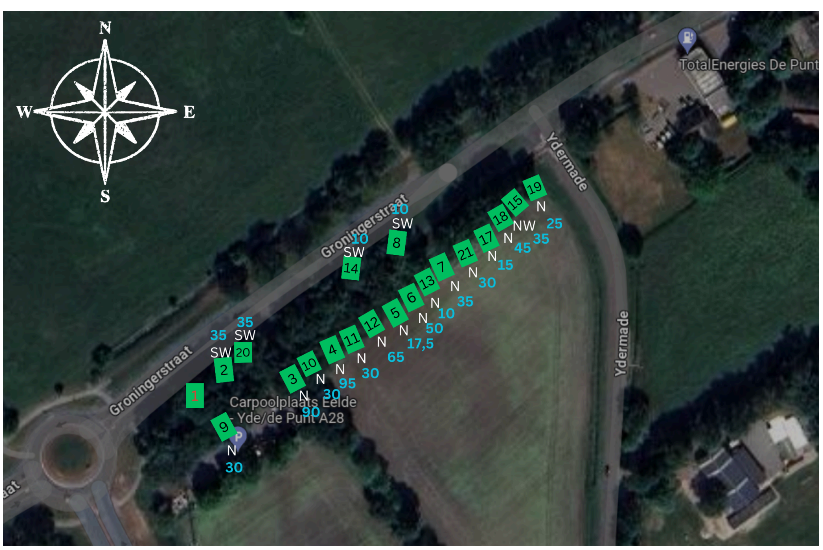

Figure 11: A map of the nest boxes in the colony of Tynaarlo and their respective fly hole orientation in white. The light blue numbers indicate the maximum percentage of paper coverage observed from the period of the 27th of March to the 12th of May. Nest box numbers marked in red indicate that nests that have not been actively occupied by jackdaws during the breeding season.

Our time series analysis aimed to define an optimal time window to research the presence of white anthropogenic material in jackdaw nests. Also, we wanted to test for paper coverage differences between breeding season stages. This analysis was conducted on occupied nest boxes in Tynaarlo due to the colony exhibiting the highest percentage of white paper coverage, where the most significant differences were anticipated. Results showed that the white paper coverage significantly decreased after the presence of chicks. Also, the incubation phase had a significantly higher coverage than the day 5 and day 10 phases. The observed decrease after hatching of the chicks implies that jackdaws no longer gather new nest material but rather remove old material. Consequently, we state that for future research, an optimal time window for the conduction of experiments ranges from the (pre-) egg laying to the incubation phase.

Throughout this discussion, several recommendations for future research have already been made. The tested hypotheses in this study include the availability, confusion, antimicrobial, and doormat hypothesis, and since none have been rejected, they require further study to draw conclusions. In Table 1, all proposed hypotheses from the literature have been summarized. Regarding the possible functionality of white anthropogenic material for jackdaws, we will briefly discuss some hypotheses we suggest for future research.

Given that the jackdaws near Glimmen breed in sheltered artificial nest boxes, one may initially assume that thermoregulation within these structures is easily managed. However, it has been proven that maintaining a stable microclimate in artificial nests can be challenging (Sudyka et al., 2022; Zhang et al., 2023). The presence of white papers might be a counteradaptation to these conditions, so we propose further examination of the potential thermoregulatory function of the white papers. Furthermore, while the nest boxes provide enough structural integrity, it should not be assumed that the incorporation of white anthropogenic material is not still an evolutionary instinctive trait regarding nest reinforcement. Future studies should investigate this possibility. Moreover, hypotheses relating to the egg phase, such as the anti-predator theory, should be prioritized in follow-up studies. Our time series analysis indicates that during this time period, the presence of white anthropogenic materials is highest, and thus, the potential function seems to be extruded during this phase. This study did not test any hypotheses regarding signaling or age. However, this might help gain more insight into the occurrence of the white materials.

In conclusion, based on this study, the research question: “Why do jackdaws incorporate white anthropogenic materials into their nests?” cannot be answered comprehensively. However, our findings indicate an optimal period for examining this phenomenon, namely from the (pre-) egg laying to the incubation phase of the breeding season. Furthermore, offering nest material using grids can potentially optimize the accuracy of observations aiming to answer specific proposed hypotheses, and this should be further investigated. Also, there seems to be evidence that the doormat hypothesis could explain the observed relationship between nest box entrance orientation and paper coverage, which should be interpreted with caution since outliers in one colony may have influenced our model. This study constitutes a framework for future research with possible hypotheses that can be explored, research setups to be used, and optimal study periods. Overall, exploring the functionality of anthropogenic materials in jackdaw nests can offer broader insights into bird behavior and adaptation as a whole.

Table 1: An overview of all hypotheses regarding the presence of white anthropogenic materials in birds nests. Both functional and non-functional hypotheses have been proposed, for the former two groups can be distinguished (nest material and signal). For further information see section 1 Introduction.

Functional
Group 1: Nest material
Thermoregulation
Nest reinforcement
Doormat hypothesis
Antimicrobial properties
Group 2: Signal
Anti-predator
Conspecific
Sexual

Non-functional
Availability
Age
Confusion

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Appendix A - Materials

Table 2: Material, company from which the respective material was obtained and a brief description of each material which was necessary for the conduction of the feather, paper and mesh experiment and nest box entrance orientation and time series analysis.

Name	**Company**	**Description**
Colored feathers	HEMA	100 colored feathers ranging from 6 cm to 12 cm. Colors include light pink, light blue, orange, yellow or green.
White feathers	Pipoos	70 white feathers ranging from 5 cm to 10 cm.
Video camera	RunCam 5	Video camera that can film for two hours
Scissors	-	For the making of similar sized feathers
White 300-gram paper	-	White pieces of 300-gram paper to tear into smaller 5 x 5 cm pieces
Chicken wire 50 cm x 5 m galvanized 25 mm	Handson	Chicken wire made of galvanized steel with a mesh size of 25 mm. The roll has a height of 50 cm and a length of 5 meters.
Binding Fix ground cover pegs	Talen Tools	3 x 10 pieces of ground cover pegs
Compass	Silva	Compass to determine nest box entrance orientation

Appendix B - Model output of orientation analysis

Table 3: Summary of the linear regression model output that tested the effect of the cosine and sine of the orientation on the percentage of paper coverage (intercept) (a). Summary of the linear regression model that tested the effect of the cosine and sine of the orientation, Tynaarlo and their interaction on the percentage of paper coverage (intercept) (b).

Model	**Covariate**	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(a) 1st model	(Intercept)	15.955	2.253	7.082	6.51e-10
	Sine_orientation	1.680	3.202	0.525	0.60139
	Cosine_orientation	8.606	2.926	2.941	0.00434
(b) 2nd model	(Intercept)	11.630	2.120	5.486	5.8e-07
	Sine_orientation	1.713	2.825	0.606	0.546
	Tynaarlo	20.067	13.227	1.517	0.134
	Cosine_orientation	2.225	3.074	0.724	0.472
	Sine_orientation : Tynaarlo	2.455	27.595	0.089	0.929
	Tynaarlo : Cosine_orientation	6.614	12.745	0.519	0.605

Appendix C - Model output of time series analysis

Table 4: Summary of the linear mixed-effects model output that tested the fixed effect of time, the presence of chicks, their interaction and the lay date on the percentage of paper coverage (intercept) (a). Summary of the linear mixed-effects model that included data points only when chicks are present and tested the effect of time on the percentage of paper coverage (intercept) (b). Estimates have been made based on the ASRT and are thus not representative of real percentages.

Model	Covariate	Estimate	Std. Error	df	t value	Pr(>|t|)
(a) 1st model	(Intercept	0.336699	0.084989	19.329038	3.962	0.000813
	time	0.001783	0.001459	160.075608	1.222	0.223458
	chicks	0.308070	0.309769	163.893849	0.995	0.321438
	Lay date	0.004574	0.006896	18.047989	0.663	0.515531
	time:chicks	-0.017881	0.013924	164.409850	-1.284	0.200881
(b) 2nd model	(Intercept)	0.708931	0.213928	13.423030	3.314	0.00538
	time	-0.019230	0.009232	11.150750	-2.083	0.06105

Table 5: Summary of the linear mixed-effects model output that tested the fixed effect of time, the presence of chicks and their interaction on the percentage of paper coverage (intercept) on a hatch date time scale (a). Summary of the linear mixed-effects model that included data points only when chicks are present and tested the effect of time on the percentage of paper coverage (intercept) (b). Estimates have been made based on the ASRT and are thus not representative of real percentages.

Model	Covariate	Estimate	Std. Error	df	t value	Pr(>|t|)
(a) 1st model	(Intercept)	0.407027	0.060303	67.164125	6.750	4.2e-09
	time	-0.001394	0.003575	102.019814	-0.390	0.6974
	chicks	-0.005830	0.064545	101.713441	-0.090	0.9282
	time:chicks	-0.015052	0.008591	101.744346	-1.752	0.0828
(b) 2nd model	(Intercept)	0.397872	0.046732	22.250862	8.514	1.89e-08
	time	0.014288	0.006021	31.068574	-2.373	0.024

Table 6: Summary of the post hoc with the Kenward-Roger method testing for significant differences between breeding phases of jackdaws. Estimates have been made based on the ASRT and are thus not representative of real percentages.

Contrast	**Estimate**	**Std. Error**	**df**	**t ratio**	**p value**
Pre_egglaying_egglaying - incubation	-0.05855	0.0473	71.4	-1.237	0.6056
Pre_egglaying_egglaying - hatching	0.00479	0.0500	71.4	0.096	0.9997
Pre_egglaying_egglaying - day5_day10	0.08162	0.0410	73.0	1.989	0.2015
Incubation - hatching	0.06334	0.0577	68.3	1.098	0.6918
Incubation - day5_day10	0.14018	0.0500	67.9	2.804	0.0325
Hatching - day5_day10	0.07684	0.0526	68.6	1.460	0.4670