The function of white anthropogenic material in jackdaw nests

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Abstract

This study looked into possible explanations for the function of white anthropogenic material in jackdaw *(Corvus monedula)* nests. Field work was performed to collect data on the percentage of the surface of nestboxes that was covered with white anthropogenic nest material, also referred to as paper coverage throughout this essay. jackdaw nest boxes near Glimmen, The Netherlands. Statistical analyses have been performed on the observational data, which found that the effect of orientation on the average paper coverage in jackdaw nests is significant, where a circular pattern was observed and the cosine of orientation had a significant influence as well. Also, the effect of breeding phases on the average maximum paper coverage was significant, with the incubation phase showing a significant difference in paper coverage compared to the combined measurements from 5 and 10 days after the hatch date of the first egg. None of the hypotheses that were tested could be rejected, however, we conclude that the most likely explanations for the function of white anthropogenic material in jackdaw nests are the so-called “doormat hypothesis”, antimicrobial and anti-predator hypotheses, since the first is related to orientation and the latter are particularly related to the absence of chicks.

1 | Introduction

Nests in general function as to “provide a receptacle in which animals can lay their eggs and/or raise their developing offspring”. (Heenan, n.d.) While long was thought that nest building was genetically determined, more recent evidence has shown that birds adapt their nest building strategies by learning. (Bailey et al., 2014)

Nest construction is a process which can involve high energetic costs and food availability seems to play a substantial role in limiting this process. (Withers, 1977)(Berg et al., 2006) In general, nests are made up of materials that function to improve the shape and structure of the nest called “structural materials” and materials which function as to optimize the microclimate of the nest cup called “lining materials”, as stated by Mainwaring et al. (Mainwaring et al., 2014a) The microclimate of the inner lining of the nest is partially determined by the design of the nest. The fitness of the parents as well as the development and growth of young can be negatively influenced by adverse conditions resulting from suboptimal nest microclimates. (Ardia, 2013; Dawson et al., 2011; Webb, 1987)

Natural selection can act on birds in several ways. A challenge for the largest fraction of birds which is present almost everywhere is avoiding predation, upon which natural selection acts to favor the ones with defensive mechanisms which decrease their chance of being predated on the most. (Withers, 1977) There are more examples of factors which influence reproductive success, like the location of the nest. Often there is a tradeoff between reducing the risk of predation and reducing the energetic costs for the construction and maintenance of nests. (Mainwaring et al., 2014) (Peluc et al., 2008). The height at which a nest is built from the ground also influences predation rates and birds have shown to determine the height at which they build their nest to predators in their environment. This has resulted in a variety of different strategies when it comes to choosing the optimal height, since conditions regarding predation rate per distance from the ground can differ from one location to another. (Lima, 2009; Martin, n.d.)

Not only natural selection, but also sexual selection can act on animals regarding their abilities to build a nest. A nest can signal and reflect aspects of an animal’s fitness and phenotypic quality through a variety of structures which aid the individual in finding a mate. (Schaedelin & Taborsky, 2009)

Nest building has been shown to be related to interactions between birds and parasites as well. A coevolutionary arms race as a result of hosts adapting to the harmful effects of parasites on their fitness has contributed to differences in nest building tactics. Parasites like mites and ticks but also fungi and bacteria can live on birds and in reaction to this, evolution has led to some birds placing green plant material, feathers and cigarette butts in their nests to counter this. (Suárez-Rodríguez et al., 2013) This is mainly done in the incubation and nestling stages of the breeding season. (Brouwer & Komdeur, 2004)(Peralta-Sanchez et al., 2010) The mechanism behind this strategy will be explained later on in the hypotheses.

Jackdaws are monogamous, particularly social birds from the corvid family which form a long-term bond with their partner. They often breed in colonies and elicit biparental care for the young, while both the male and the female contribute to building the nest similarly as well. They differ to some extent in their roles when potentially dealing with competition for nest locations, where females contribute on average more to the construction of the nest while males spend more time in vigilance. (Hahn et al., 2021)
They build their nests within cavities, in which a platform can be made of structural materials like sticks and a cup makes up the inner section, existing of lining materials like for example grasses, mud and animal hair. (Hahn et al., 2021) Clutches are produced once a year, one at a time. (Henderson & Hart, 1993)

Several studies on different bird species have shown that birds incorporate anthropogenic waste into their nests. This potentially carries health risks for the birds and can ultimately increase mortality due to entanglement for example. (Jagiello et al., 2019) Information on this topic is scarce, as research has mostly been directed at atmospheric pollution rather than solid waste. (Jagiello et al., 2022)
Jackdaws (*Corvus monedula*), are one of the species in which this behavior has been observed. Near Glimmen, The Netherlands, colonies of jackdaws in artificial nest boxes, as well as several solo-nest boxes have been monitored and observations were made of the inside of their nest boxes. White pieces of paper have been found in their nests, but it is not yet entirely understood for jackdaws, but also for birds in general, what the function(s) of these pieces of white anthropogenic material are, what mechanism drives these birds to incorporate them in the nest and how the parents' and chicks' fitness is affected by these pieces. (Jagiello et al., 2019) This has led us to the main research question:

"What is the function of white anthropogenic material in jackdaw nests?"

There are several hypotheses to what the function of white anthropogenic material might be for jackdaws and birds in general. These can be divided into two groups, namely the group which proposes that the material has a function and the group which states that it does not have any function. The functional hypotheses can be subdivided into two groups, of which the first is the group which poses that the white anthropogenic material is used as nest material to optimize the structure or microclimate in the nest. The second group poses that the material acts as a signal between one jackdaw and another, or between a jackdaw and a predator.

Table 1: The hypotheses for the incorporation of white anthropogenic material into nests by jackdaws, divided into functional and non-functional.

Functional	**Non-functional**
Group 1: Nest material	Availability*
Nest reinforcement	Age
Thermoregulation	Confusion*
Doormat hypothesis*	
Antimicrobial properties*	
Group 2: Signal	
Sexual	
Anti-predator	
Conspecific	

* *Hypothesis was tested in this study*

Functional hypotheses

Group 1: Nest material

Nest reinforcement

to strengthen the nest structure with plastic strings (Antczak et al., 2010)
The most common role of debris is its practical use in nest building, as a constructional or/and padding material (84%). (Jagiello 2019) An example of this is the strengthening of nest structure with plastic rings in the Great Grey Shrike *(Lanius excubitor).* (Antczak et al., 2010) Since Jackdaws in the colonies near Glimmen breed in artificial nest boxes, this would

likely decrease their need for strengthening the structure of the nest, as it is unlikely to collapse or fall.

Thermoregulation

Nest structure and materials have been shown to affect the temperature within the nest. (Corimanya et al., 2024) Birds select for materials that aid in the regulation of the nest temperature so that conditions approach optimality for the development of their young, egg incubation and for their own body temperature, through either keeping heat or reflecting light and cooling down. (Deeming et al., 2020; Hansell, n.d.; Olborska & Kosicki, n.d.) Anthropogenic materials have been suggested to influence nest insulation properties. (Corrales-Moya et al., 2021; James Reynolds et al., 2019) The insulational properties of nests in artificial nest boxes might be different than for jackdaws breeding in natural circumstances. If white anthropogenic material functions as to regulate the temperature of the eggs, it would seem likely to find the material in the inner lining of the nest cup where the eggs are located, but this observation would not proof this hypothesis since there could be other reasons for the white anthropogenic material to occur near the eggs.

Doormat hypothesis

Orientation of the entrance of nests has been shown to have an effect on the temperature and humidity within nests. (Corimanya et al., 2024) Apart from the fact that a more humid nest would likely offer more possibilities for funghi to grow, water also has a much higher heat capacity than air, thus it would be likely that nests cool down and heat up more quickly when humidity is relatively high, proving suboptimal for regulating the optimal temperature for the eggs and young. Since the predominant wind direction in the Netherlands is South West, it is advised to orient nest box entrances in the opposite direction, towards the North East. (Vogelbescherming Nederland) We therefore suspect that the average maximum paper coverage would be highest in nest boxes with an entrance that is oriented towards the South West, since winds would carry moist in through these holes the most. Since the white anthropogenic material which is observed in the nests near Glimmen is often likely to be able to absorb moisture, as most of it is paper or other fabrics, these materials might play a role in regulating the humidity of the nest.

Antimicrobial/parasite resistance

Bacteria potentially cause reduced viability of the embryo and increase the chance of infection of the shell. (Cook et al., 2003, 2005; Soler et al., 2012) Antimicrobial resistance has been shown to be a potentially plausible explanation for the incorporation of, mainly white but also sometimes coloured, feathers into bird nests. Evidence for this theory was found in nests of barn swallows and it is suggested that antibiotic agents produced by bacteria that grow on feathers play a role in this. These bacteria outcompete other, sometimes harmful, bacteria by using the present keratin, which is an important component in feathers, to fuel their metabolism. (Ruiz-Castellano C, 2016) Experimental manipulation of the feathers in the lining of nests of barn swallows has shown to alter the composition and anbundance of bacteria on eggshells when feathers came in contact with the eggs (Peralta-Sanchez et al., 2010) and addition of white feathers at the start of the incubation phase increased hatching success. (Peralta-Sanchez et al., 2011) Although white pigmented feathers increased relative to colored feathers over time as the breeding season progressed, most of the nests contained both types of feathers. This, together with the fact that antimicrobial activity also belongs to pigmented feathers, which have also been shown to increase phenotypic quality of spotless starling chicks, and the fact that experimentally added feathers in barn swallow nests increased the antimicrobial activity of bacteria from unpigmented feathers (Peralta-Sánchez et al., 2014), allows for speculation on the possibility that certain combinations of pigmented and unpigmented feathers maximize antimicrobial activity. (Ruiz-Castellano et al., 2018) Also, one study showed that debris can act as an ectoparasite repellent due to its toxic substances (Suarez-Rodríguez et al., 2013).

Group 2: Signal

Sexual

If jackdaws show to actively include feathers in their nests, this could be potentially explained by sexual selection. Research in Spotless starlings has shown that those birds bring feathers to the nest as a reaction to males carrying green plants. They also found that the stage mattered, with a higher abundance of feathers during the laying stage than during the pre-laying stage. They proposed that this could be an indication of feathers acting as a female signal to stimulate paternal care, as this phase is closer to the energy-demanding early nestling stage, as did other studies. (Conover, 2024)

Anti-predator

Another way in which the white anthropogenic material could be used as a signal is to disrupt the vision of a predator to make it harder to detect the eggs. This hypothesis was described by Hansell, and further tested with the use of experiments including white paper and chalk spots, and multiple types of analyses were performed. (Hansell, n.d.) Although predation rates were not affected, lower location rates were found in a photo-based visual search experiment for natural nests with white spots than without white spots, while contrasts between different visual elements of nests significantly increased as well. The conclusion was that white objects could potentially work as a way of camouflage via disruptive camouflage, which mitigates predation rates by disrupting the outlines of for example an egg or an animal and creating an illusion of an object in which a predator would not be interested through increasing the contrast between objects in the nest. (Mulder et al., 2021)

Conspecific

White anthropogenic material could also be a way to signal to other jackdaws. It could provide other jackdaws with information on the quality of the individual that has occupied a certain nest. (Sergio et al., 2011). (Jagiello 2019)

Nonfunctional hypotheses

Availability

The first non-functional hypothesis is the availability hypothesis, which states that human activities lead to a higher coverage of anthropogenic white material in nests. This is linked to a decrease in natural nest materials which leads to an increase in the likelihood for birds to incorporate anthropogenic materials in their nests as the availability of those anthropogenic materials is relatively higher. (Jagiello et al., 2022)

Age

The age hypothesis states that there is a link between the age of the bird and the extent to which the bird incorporates anthropogenic materials in its nest. This assumes that age is related to individual experience, as the individual becomes more experienced when becoming older. (Jagiello et al., 2022)

Confusion

The last hypothesis poses that birds might mistake the white anthropogenic material for edible items, for natural nest material or confuse them with their eggs. (Conover, 2024) (Korte, 2023)

To test these hypotheses, we conducted experiments in the field and performed analyses on the obtained data from those experiment, as well as on data from already existing datasets from the colonies in Tynaarlo from previous years. (Verhulst Group) We followed a multifaceted experimental approach to investigate the behavior as well as the preferences of jackdaws in the light of nesting materials. We performed field experiments, observational analyses and statistical analyses to find an answer to the question what the function of white anthropogenic material in jackdaw nests would be. The hypotheses we tested were chosen based on a combination of criteria, including how well the time and materials allowed us to perform experiments and analyses, and for some of the hypotheses we chose those seemed the most likely to be true based on the information in the literature we found. We therefore chose to test the doormat hypothesis as data on paper coverage and orientation were possible for us to collect and analyse based on named criteria, and research has shown a link between orientation and humidity. Datacollection for the antimicrobial properties and availability met the criteria as well for the same reasons. The confusion hypothesis did not seem likely to be true, but it seemed fairly easy to test with the data and observations from the experiments.

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 off 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 (Fig. 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.

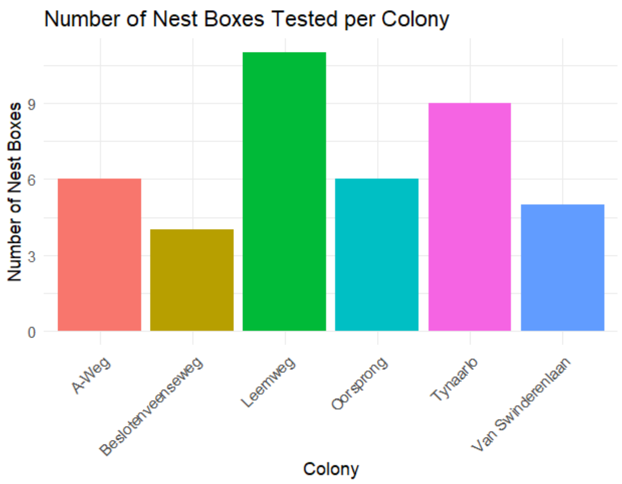


Figure 1: Bar plot of the total number of nest boxes on which feather manipulations were performed, grouped by individual colonies.

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 of the company RunCam 5 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 10th 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

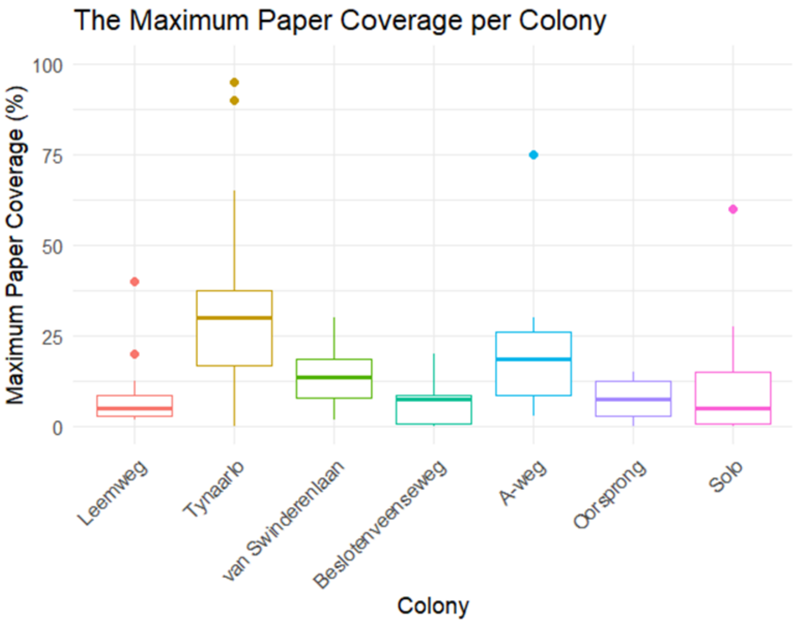


Figure 2: Box plot of the maximum observed paper coverage in nest boxes grouped by colony. Solo boxes have been grouped together.

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

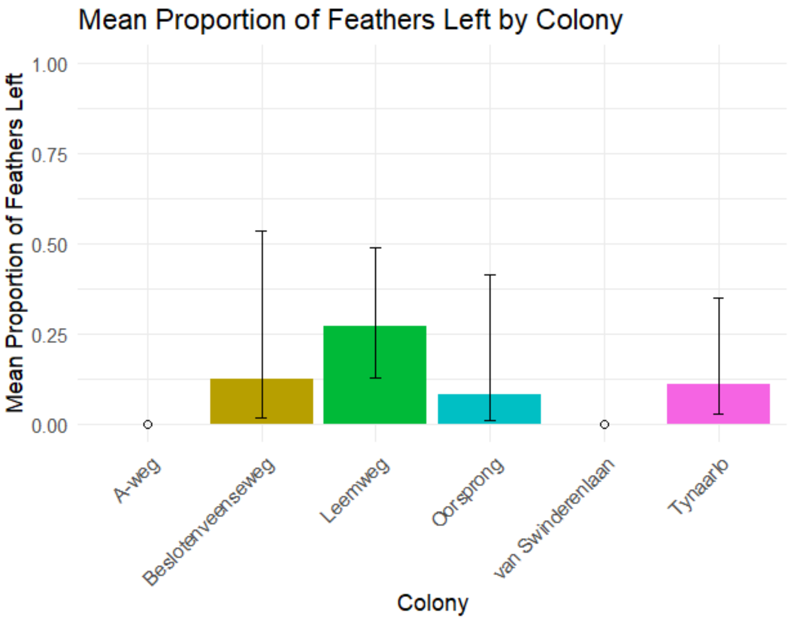


Figure 3: Bar plot of the mean number of feathers left after three days as a proportion of the number of manually supplemented feathers, grouped by individual colonies. Black lines indicate the 95% confidence interval. Circles show that no confidence interval could be calculated, which occurred only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

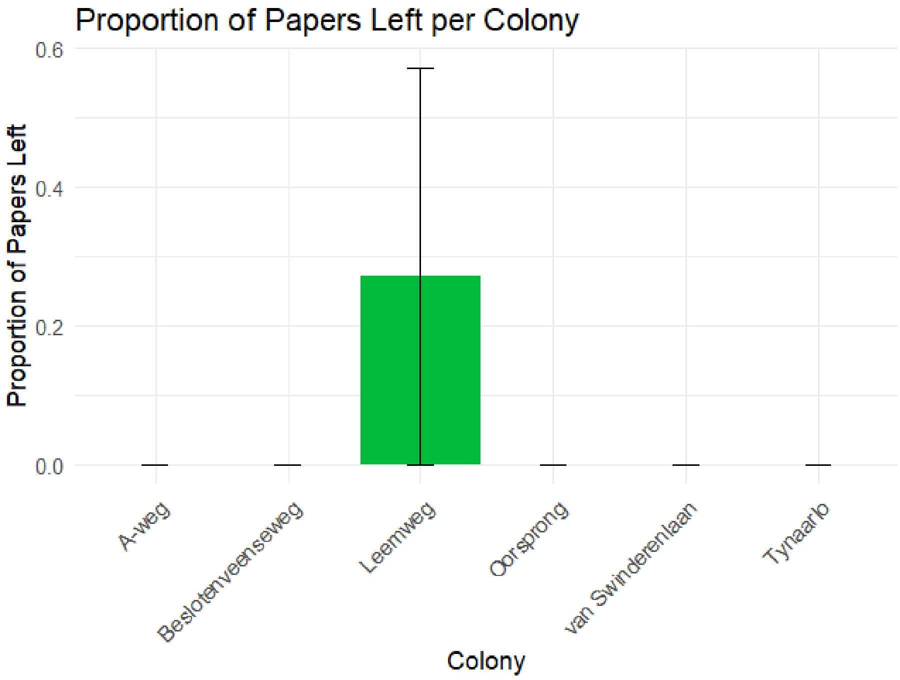


Figure 4: Bar plot of the number of pieces of paper left after two days as a proportion of the number of manually supplemented pieces, grouped by individual colonies. Black line indicates the 95% confidence interval.

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 (Fig. 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 (Fig. 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

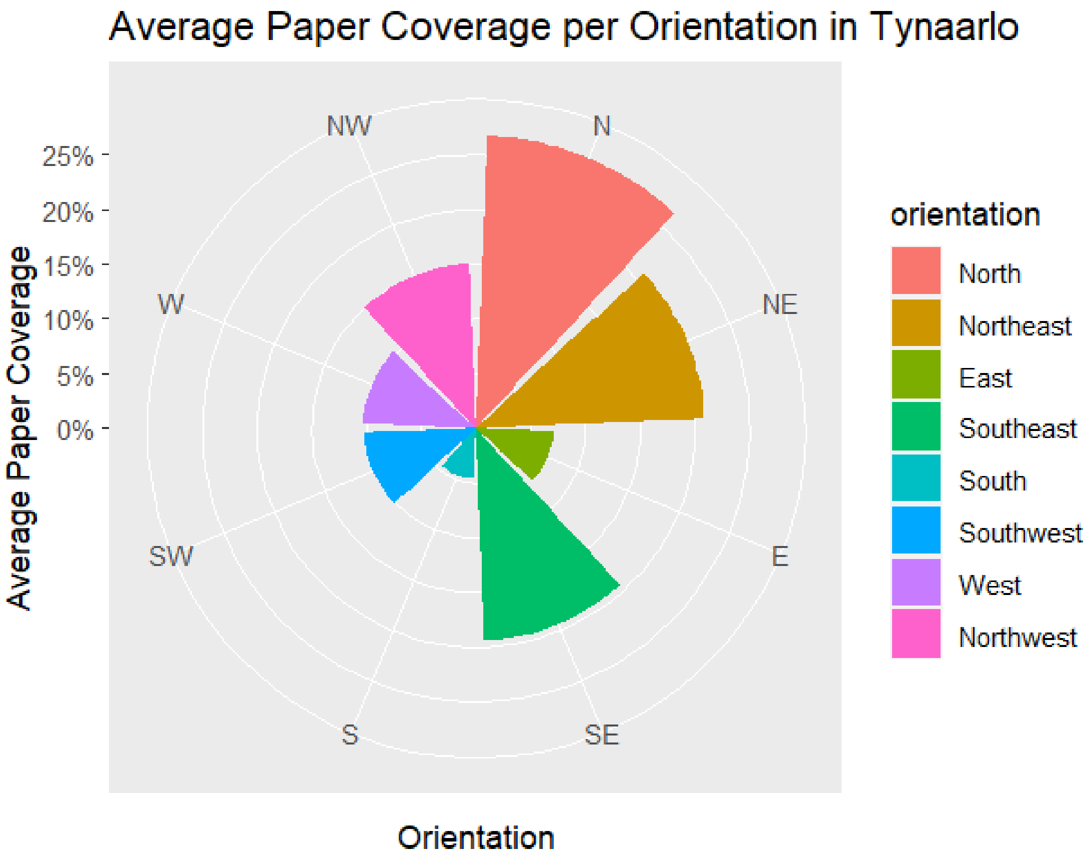


Figure 6: Circle diagram of the mean paper coverage in the colony of Tynaarlo, grouped by orientation. Each orientation constitutes an angle of 45º.

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

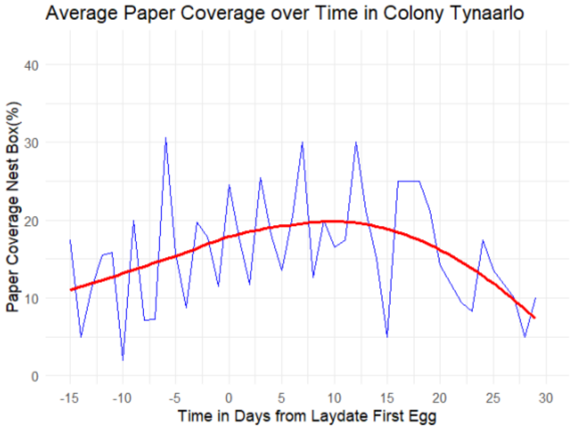


Figure 7a: The mean paper coverage in the colony of Tynaarlo over time with the lay date of the first egg as t= 0. The red line represents the trend and the blue line represents the mean paper coverage for each day

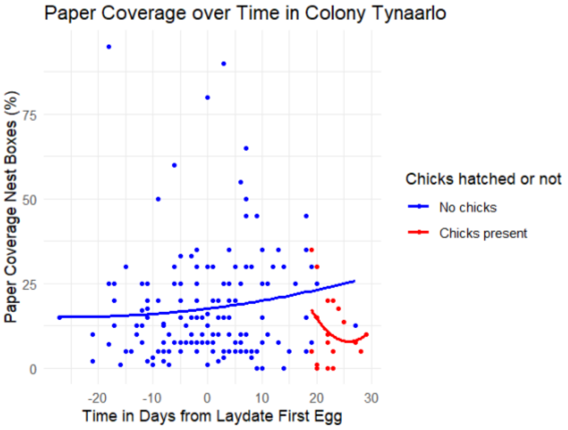
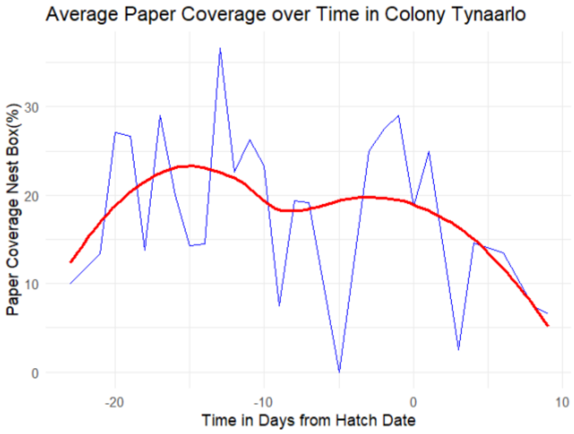


Figure 7b: The paper coverage in the colony of Tynaarlo over time with the lay date of the first egg as t= 0, grouped by the presence or absence of chicks. Dots represent individual data points and the lines represent trends. Dots correspond to nest boxes sampled multiple times.

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.



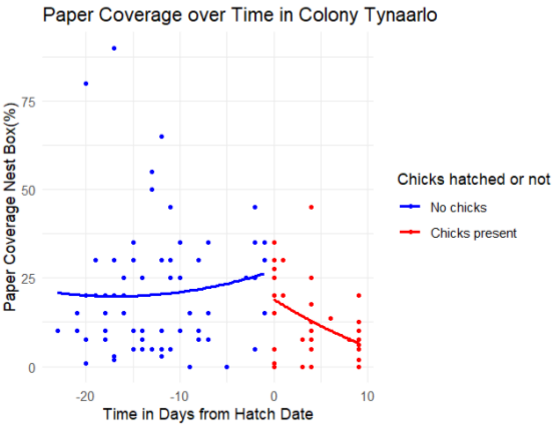


Figure 8a: The mean paper coverage in the. Colony of Tynaarlo over time with the hatch date of the first chick as t= 0. The red line represents the trend and the blue line represents the mean paper coverage for each day.

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.

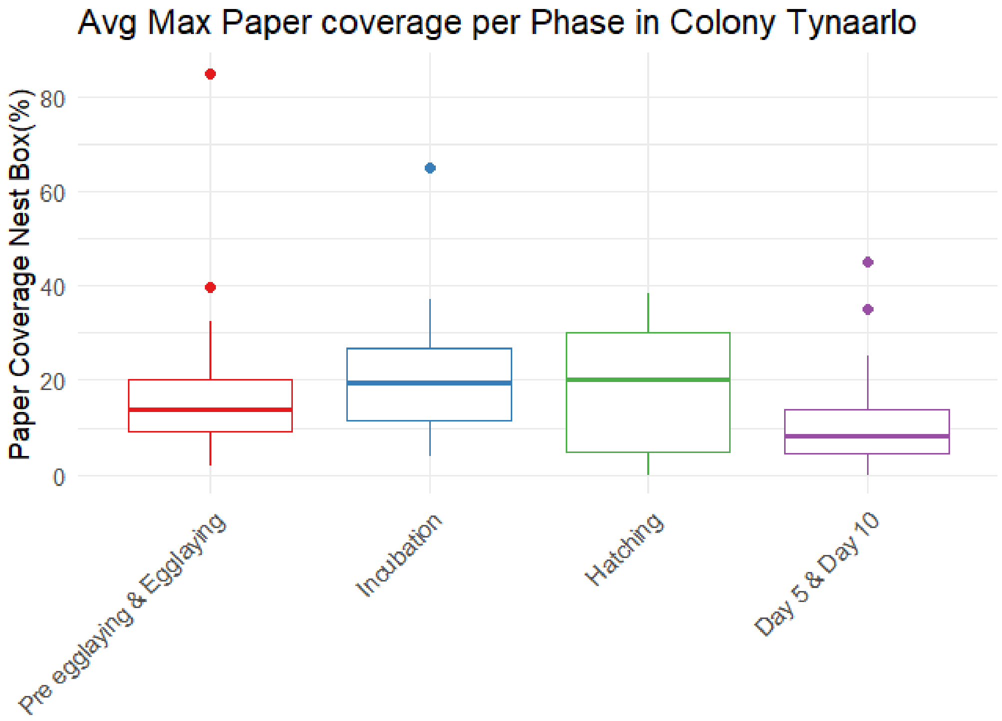


Figure 9: Boxplot of the mean of the maximum paper coverage in colony Tynaarlo, grouped by phase.

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

Feather & paper manipulation

The aim of the feather manipulations was to test the availability, antimicrobial and confusion hypotheses. No analysis has been done, therefore none of the hypotheses could be rejected and further research should be done to test the likelihood of these theories. However, active management was observed, since 72/82 feathers were removed from the nests. Due to this finding, it is possible that due to the supplementation of feathers, the level of acceptance of foreign objects in jackdaws was tested, which made the results less informative for the other hypotheses.

The proportion of feathers (10/82) that were left were relatively low. This does not seem like a strange result when you consider the influence of human interference on the level of acceptance. Nothing could be concluded about the possibility of the availability hypothesis.

If the antimicrobial hypothesis were true, a relatively higher propotion of feathers would be expected in the inner lining of the nest. (Peralta-Sanchez et al., 2010) 8/10 feathers were found in the outer lining, this variation was not significant however, but since there seems to be a slight preference for the outer lining this could possibly be an indication that the antimicrobial hypothesis does not hold for the feathers. It would also be expected that jackdaws show a preference for white feathers over colored feathers due to their relatively higher antibacterial capacities, but the variation in colors was not significant. It could be that jackdaws show no preference for white feathers over colored feathers since certain combination of both colored and white feathers have been shown to decrease antibacterial loads on eggshells more than only white feathers. (Ruiz-Castellano et al., 2018)

The copulation which was observed after inspection of the feathers could indicate that feathers have a function related to sexual signals, e.g. stimulating the other partner as a courtship display. However, this could be more of importance for mate choice, which has already been established in the jackdaw pairs. (Schaedelin & Taborsky, 2009) (Ruiz-Castellano et al., 2016)

If the confusion hypothesis holds, it would be expected that jackdaws show similar behavior towards white anthropogenic material as to feathers and therefore, if the antimicrobial hypothesis and/or availability would hold for the feathers, this would result in a pattern in coverage and placement of white anthropogenic material in nests that fits the expectations according to these hypotheses. Whether this is the case could not be concluded from this experiment.

The aim of the paper manipulation experiment was similar to the feather manipulation experiment, i.e. we tested for the availability, antimicrobial and confusion hypotheses. No analysis has been performed for similar reasons as in the feather manipulation experiment and no hypotheses could be rejected or scored for their likelihood. Again, the amount of materials that we supplemented and found back was relatively low (3/41), most likely for the same reasons as with the feathers. The marked piece of 300-gram paper which was found in another nest box within the same colony could indicate that jackdaws might preferentially incorporate the paper in their nest when they can actively select it, since it has most likely been thrown out by the couple where we initially supplemented the paper. This might indicate active management and a low level of acceptance of the jackdaw that removed it for items that are supplemented by humans. No activity was caught on camera, which was most likely due to the fact that the cameras did not record long enough. To ensure the capture of activity on video footage, more cameras and a longer recording time would be more optimal.

Mesh experiment

The mesh experiment was performed to test the same hypotheses as the paper and feather experiments. However, no activity was observed of the jackdaws towards the feathers and paper pieces in the meshes. This is likely because the experiment was not performed in the optimal breeding phase, since many pairs were already in or near the hatch phase, when paper coverage showed the largest decline. The mesh set up could prove to be more optimal than manual supplementation since it allows for active selection, however, these type of experiments should be conducted well before the hatch phase in order to find evidence for the optimality of this technique and more informative data on the differences and similarities in behavior of jackdaws towards feathers and paper pieces. To conclude, the research setup has not been optimized with this experiment but future research during the incubation phase is needed to further test the efficiency of this method, as well as the availability, antimicrobial and confusion hypotheses.

Nest box orientation analysis

The aim of the nest box orientation analysis was to test the doormat hypothesis. The model with the effect of orientation on paper coverage was significant, which is congruent with the expectations based on the work on Grasshopper Sparrows (*Ammodramus svannarum*) and Eastern Meadowlarks (*Sturnella magna*). (Corimanya et al., 2024) It seems likely that jackdaws either adapt the amount of white anthropogenic material in their nest to the orientation of the nest box entrance, or that this is a remnant behavior which has evolved to optimize the microclimate of their nest in natural situations but is still displayed in the situation with artificial nest boxes. We found a significant effect of orientation on the average paper coverage in Tynaarlo, indicating that there is a pattern that can predict the average paper coverage on a circular scale in this colony. Whether this holds for other colonies should be looked into in further research. The cosine of orientation significantly affected paper coverage and therefore seems to be a fairly good predictor of paper coverage which might prove useful for future research and conservation work. The distribution we found seemed opposite to our expectations, since the highest average paper coverage was observed in the northern orientations, while the southern directions showed the lowest coverage. This might have to do with our assumptions, since they likely differ from the real situation, as we assumed winds to come in from the South West on average but this could have been different. Another factor which might have influenced the results could be day by day differences in precipitation. The second model which tested the influence of Tynaarlo was significant as well, but none of the individual covariates showed a significant effect. However, Tynaarlo increased the intercept of 11.63, indicating average % paper coverage, by 20.067, thus showing a substantial positive effect. This was mostly due to the fact that in the colony of Tynaarlo, paper coverage was substantially higher for a large fraction of nest boxes than in other colonies, combined with the fact that many nest boxes had an entrance facing towards the north(west). Correlations and such between the covariates in the model might have caused the statistical test to behave differently, explaining the significance of the model but insignificance of the individual covariates. To conclude, from our experiment the doormat hypothesis could not be rejected, however we think that this hypothesis is most likely to explain the largest amount of variation compared to the other hypotheses which we tested. There seems to be an interaction between orientation of the nest box entrance and the paper coverage, which should be further investigated as it could aid in testing the doormat hypothesis.

Time series analysis

The first analysis on the effect of lay date on the average paper coverage in Tynaarlo initially showed a clear quadratic relationship with an initial increase and eventually a decrease in paper coverage, which matched our expectations based on observations of nest boxes near Glimmen in previous years. The ICC value of 0.35 showed that there is quite a substantial amount of differences in behavior between jackdaws from different nest boxes. The second model showed a negative trend in paper coverage after the chicks hatched. Similar results were obtained for the analysis with the hatch date, but this time the second model including only data after the hatch date found a significant decrease of paper coverage when chicks were present. Further analysis showed a significant difference between the incubation phase and the combined day 5 and day 10 data, indicating that the average maximum paper coverage is the highest in the incubation phase. Therefore, it seems that the most optimal timing for research on white anthropogenic material in jackdaw nests would be during the incubation phase. However, additionally conducting experiments during the pre-egglaying and egg-laying phase could prove benficial as well to observe a broader pattern. These results could also indicate that the anti-predator and antibacterial hypotheses are most likely to explain the observed variation in paper coverage and ultimately the function of white anthropogenic material in jackdaw nests, since these are linked to the presence of eggs and absence of chicks, but further research should be conducted to investigate this.

To conclude, we found a significant effect of orientation on the average coverage of white anthropogenic material in jackdaw nests in a colony near Glimmen. We also found that research on this matter could best be conducted in the period before the hatching of chicks. From our results, the function of white anthropogenic material in jackdaw nests seems most likely to be related to the doormat hypothesis and/or one of the hypotheses that are linked to the presence of eggs, namely the anti-predator and antibacterial hypotheses. However, we could not reject any of the other hypotheses and the preference for white over other colored pieces of anthropogenic remains unanswered, so more research is needed to find a definite answer to what the function might be. This is important because finding the function can aid in the understanding of jackdaw behavior in relation to pollution, which is a problem that does not seem likely to disappear shortly, and ultimately the conservation of jackdaws and maybe even other species which come in contact with anthropogenic waste.

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Rosa Korte, “The Use of Foreign Objects in Birds’ Nests”, Bachelor Thesis, University of Groningen, Faculty of Science and Engineering, Biology, Ecology and Evolution, Supervisor: Prof. dr. S. Verhulst

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