Uncovering the hidden:

The role of UV light in moth camouflage

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Research Project Ecology & Evolution 2 - WBBY906-10.2022-2023.1

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05/06/2023

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1. Abstract

Up until now, a lot of research has been done on cryptic and disruptive camouflage in moths. However, to what degree moth species use UV reflectance present in their wings as camouflage, has not yet been thoroughly researched. To answer this question a field study was conducted. Models were made resembling a moth using a mealworm as its body and a paper print of a pattern of either *D. elpenor* or *P. muscerda* as wings. Half of the models were treated with a UV reflective ink, while the other half remained untreated. Models were placed in a gradient of 0 to 30 meters from the waterbody for 30 hours, at which every 6 hours they were checked if they were predated. The models resembling *P. muscerda* showed that predation at proximity three (30 meters) was significantly lower than at proximity one (0 meters). Furthermore a significantly higher positive effect of UV treatment on predation at proximity three than at proximity one was observed for these models. However, when looked at the models resembling *D. elpenor*, no significant differences were observed. From this it can be concluded that the brighter colored species, like *P. muscerda*, can indeed benefit from having ultraviolet reflection in their wings. This however, cannot be said about the darker coloured species as the brown variants did not show any significant differences.

2. Introduction

2.1 Camouflage

Camouflage is a very common method of survival used by many animal species. Three forms of camouflage are mimic, cryptic and disruptive camouflage. When an organism uses mimicry, it has certain colors that will resemble other organisms that are dangerous to the predator (Rota, & Wagner, 2006). This way they try to resemble another animal that is toxic for example. Within cryptic camouflage the organism's skin, scales, feathers or fur has colors that match the surroundings of the organism (Kang et al, 2012). This way it will go unnoticed by potential predators, as the organism will blend in perfectly with its surroundings. Disruptive camouflage relies on high contrast coloration that will break up the outline of the organism (Stevens, & Merilaita, 2009). This results in the predator not being able to recognise the organism as prey. Cryptic camouflage, as well as disruptive and mimic, are regularly found within nocturnal Lepidoptera species (Kang et al, 2012;Rota, & Wagner, 2006;Schaefer, & Stobbe, 2006), as they often fall prey to predatory bird species such as Great tit and Black bird (Schaefer, & Stobbe, 2006).

2.2 UV reflectance

However, moths also possess other adaptations in their wing coloration. One of these is the UV reflectability that is present in the scales of their wings. The scales of many species reflect this ultraviolet light (320-400nm) and it is most common in nocturnal species (Lyytinen et al, 2004). The reasoning behind this UV reflectability is still up for debate, however within diurnal butterflies it has been hypothesized to be a way of communication (Burghardt et al, 2000; Silberglied, & TaylorJr, 1978). To add to that, a link has been hypothesized between habitat types and UV reflectance of lepidoptera species. It was found that specimens in a hydrophilous environment tended to have a higher UV reflectance than specimens in a drier environment (Zapletalová et al, 2016). Birds have adapted to this ultraviolet light and have developed special cones in their eyes, making them capable of seeing ultraviolet light (Bennett, & Cuthill, 1994; Cuthill et al, 2000). As the surroundings of the resting moths do not reflect a great amount of UV light, they will become an easy target for these birds. Nonetheless, water bodies and moist vegetation tend to create a high ultraviolet reflection (Cezário et al., 2022). Thus it could be hypothesized that species with a high uv reflectance are more conspicuous compared to species with a low reflectance, as they tend to blend in better within an humid environment where lots of UV light is reflected.

2.3 Hypothesis

A study was conducted to investigate to what degree ultraviolet reflectance in the wings of nocturnal lepidoptera can function as a form of camouflage. As earlier research already Showed a relationship between the UV reflectance of the wings of a species and the humidity level within their habitat, it was concluded that species with a higher UV reflectance tended to live in habitats with a higher humidity (Zapleptova et al., 2016). As UV light will be reflected less by its surroundings, models with UV reflectance would stand out more to the predatory birds than models without UV reflectance (Lyytinen, A. et al, 2004). Therefore it is hypothesized that the moth models with UV reflectance, placed in the habitat closest to the waterbody, would have a higher survival than moth models without UV reflectance. Furthermore, it is expected that at habitats with a lower humidity level, so at a distance of 30 meters from the waterbody, predation on models with UV treatment will increase compared to untreated models.

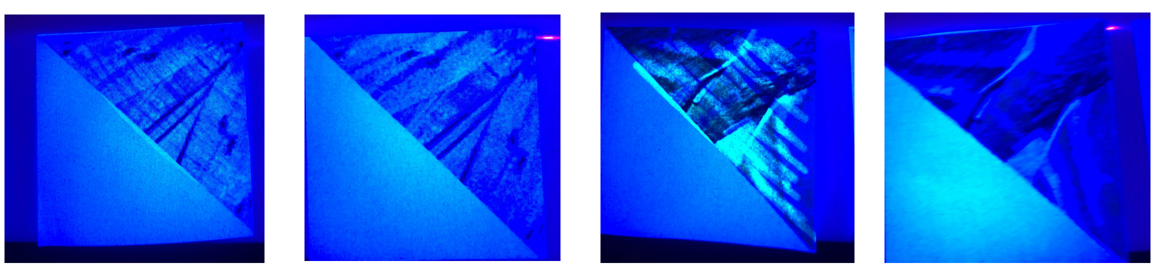
3. Methods

3.1.1 model species

The models were created using two moth species, *Deilephila elpenor* (Elephant hawk) and *Pelosia muscerda* (dotted footman). These species were chosen for their difference in habitat and UV reflectance as well as their different camouflage techniques. As *P. muscerda* tends to reside in habitats with swamps and water present (e-Vision.nl, The Netherlands, n.d.; Spitzer & Jaroš, 2009) and also having a high UV reflectance (Zapletalová. et al, 2016), while *D. elpenor* prefers grasslands (e-Vision.nl, The Netherlands, n.d.-a) and has a low UV reflectance (Zapletalová. et al, 2016). The hawkmoth also resembles the colors of the tree bark (mimic), while the dotted footman has more disruptive colors.

3.1.2 Design

The patterns of these species (pictures from vlinderstichting.nl & waarneming.nl) were put into a triangle, using the app Canva (version 4.64.0), to create a simple moth shape from 62 mm by 34 mm (HxW). The models were printed on paper and the blank triangle was glued to the back for sturdiness. To create models that will have UV reflectance, special pens containing invisible ink were used, whereby the entire surface of the model was covered in ink. The ink was applied all over the models, to enhance the chances of seeing an effect of the UV reflectance. With an UV light the models were checked whether or not the invisible ink covered the model sufficiently (Figure 1). If sufficient the models were left to dry for a night. Following this, two trial runs were performed using the models without UV treatment at the locations to ensure birds would predate on these models nonetheless. These trial runs were successful and thus these locations and models were chosen.



A B C D

Figure 1a,b,c,d: From left to right: P. muscerda with UV ink, P. muscerda without UV ink, D. elpenor with UV ink, D. elpenor without UV ink

3.2 Determining location

3.2.1 Orientation

To be able to say anything about the UV reflectance of the environment, humidity measurements were done. To create a humidity gradient and therefore a UV reflectance gradient, an area was chosen for the provinces Drenthe, Groningen and Friesland. Drenthe had two sites and Groningen and Friesland both acquired four sites. Each area consists of three proximities whereby proximity one was closest to the waterbody, proximity two was 10 m from the waterbody and proximity three was 30 m from the waterbody. These proximities were chosen due to restrictions of the locations, regarding location of trees or accessibility.

For every proximity, two trees of the same species and around the same diameter were chosen to serve as placement of the moth models. All the trees used, although not always the same species, were brown.The proximities were located on the south side of the waterbody, as the sunlight, and thus the UV radiation, comes from the north for most of the day.Six trees per area were used, Drenthe had two areas and therefore 12 trees, both Friesland and Groningen had four areas and therefore 24 trees.

3.2.3 Fauna

Since birds were a necessity for this experiment to succeed, the presence of three bird species was taken into consideration too. Bird species that had to be present were Black bird (Turdus merula), Great tit (Parus major) and Blue tit (Cyanistes caeruleus). These species were selected for, given that all three species are insectivorous and are all fairly common within the Netherlands. Bird species that were present (Appendix, Table 1), as well as predatory insects present on the moths (Appendix, Table 3) and tree species used (Appendix, Table 2), were written down.

To give a short description of all habitats: The location in Drenthe was located next to a frequently used dog walking pathway, in a moderately open area. Birds were abundant here as were oak trees. The location in Friesland resembled Drenthe in the amount of recreation and density of vegetation. At this site vegetation mainly consisted of birch trees, beech trees and some scattered pine trees The location in Groningen however, was denser in vegetation compared to the other two locations, it was also less likely to be disturbed by visitors as models were hung away from the small walking path that was present Pictures of these areas were added to the appendix to show a general overview of the habitats present at the sites.

3.3 Model placement and measurements

3.3.1 Placement

For the placement of the models, the south side of the tree was chosen. During experimental trials, it was observed that most of the bird species foraged from the trees for prey, instead of foraging in flight above the waterbody. This resulted in placing the models on the south side of the trees, to create maximum possibility for predation. As there was only water on the north side of the trees. To make it accessible for every participant to pin the models down, a height of 1.60 m was chosen. With a steel pin, the model was attached to the tree with a mealworm, which functions as the body of the moth.

The first measurements for *D. elpenor and P. muscerda* were taken at the 8th till 9th and 11th till 12th of May 2023 For these dates, all the trees located at the left of the waterbody had models with UV ink and all the trees on the right had models without UV ink. On the 8th of May, at 7:00 the first measurements started with models of *D.elpenor* and lasted till the 9th of May at 19:00. On May 11th the second measurements started at 7:00 with models of *P. muscerda* and lasted till May 12th at 19:00. During the second week of measurements from the 15th to the 16th of May and 18th till 19th of May, the placement of models was switched, whereby trees on the left of the waterbody had models without UV ink and the trees on the right had models with UV ink.

3.3.2 Measurements

Every six hours, the trees were checked. Creating a schedule of 7:00, 13:00 and 19:00, the next day the same schedule was continued. Between 19:00 and 7:00 the next day ,no measurements were taken, since this period contains a total of approximately four hours of sunlight, resulting in the birds being inactive for the largest part of this period. Additionally, the weather conditions of that exact six hour period were written down, using the weather app of Apple and specifically Buienradar for accurate precipitation. The conditions that were measured were the UV index, the precipitation, temperature, wind direction and wind speed. The precipitation was the sum of all the precipitation over the last six hours. These parameters were chosen, because temperature and precipitation influence the activity of other prey items nearby (Drakou et al., 2020; Siikamäki, 2008)) and therefore also influence the chances of a bird predating on the model. The parameter of humidity is influenced by the wind, as strong winds have a chance of bringing in air with a higher or lower humidity from other locations. To get accurate measurements of humidity of the different gradients, a humidity and temperature machine from the brand PARKSIDE was used. Measurements with this machine were performed as follows: the machine was placed out of the wind at the height of the hip, in front of the body with the back against the wind to rule out any influence from wind and breathing as much as possible. When values stabilized or after 5 minutes the results were written down.

3.4 Statistical analysis

For the statistical analysis, the data were analysed using the Cox's proportional hazards survival regression test and additionally the concordance, likelihood ratio test, Wald test and score (logrank) test were performed. These tests were conducted using the program R Studio (version 2021.09.2.382). To get a clear vision of which effect variables like proximity and treatment have independently, a survival probability plot was made for both variables. Furthermore, a survival probability plot was made including both the variables treatment and proximity.

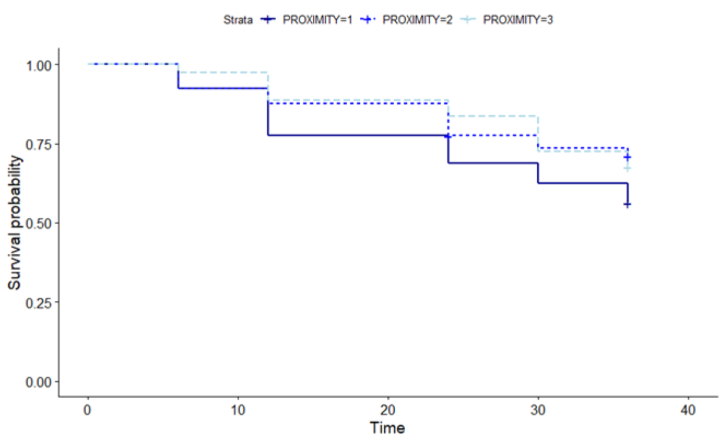
Firstly, the Cox's proportional hazard test was used to test the effect each measured variable had on the predation risk individually, while controlling for all other variables. The variables that were tested were: proximity (to the waterbody), treatment (UV or normal), wind direction, wind speed, temperature, total precipitation, site and model species. Secondly, the effect of the interaction between treatment and proximity on predation risk was tested, controlling for wind direction, wind speed, temperature, total precipitation, site and model species. To detect whether or not the effect of the UV treatment on predation differed per proximity. Because the different proximities did not result in the expected humidity gradient, proximity might not be a good substitute for habitat UV reflection. Therefore, in the third analysis the humidity measurements taken in the field were used instead of the proximity. In this analysis the effect UV treatment has on predation for different humidities was tested, controlling for wind direction, wind speed, temperature, total precipitation, site, model species and proximity. Given that the two model species were found to have significantly different predation risks, the fourth model was used to test if the effect of the interaction between proximity and treatment was different between the two species models. What was tested here was the difference in the effect the treatment has per proximity on predation between the two model species, controlling for humidity, wind direction, wind speed, temperature and total precipitation.

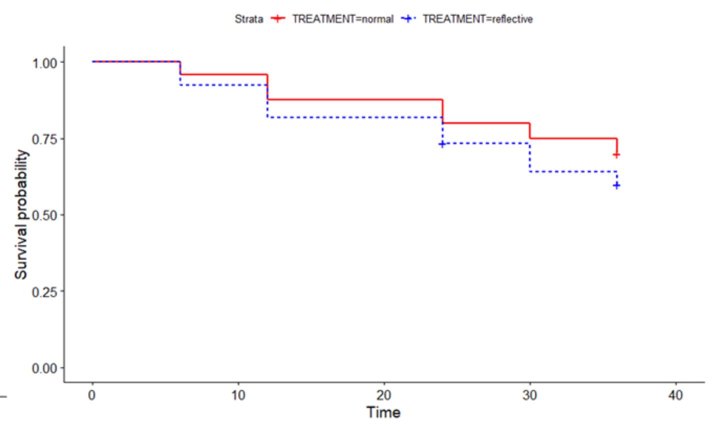
Since the effect of treatment per proximity on predation was found to differ just not significantly between the two species, the fifth analysis consists of two models used to test if the interaction between treatment and proximity has an effect on the predation of the two species on their own. So, these models tested the effect treatment has per proximity on predation of the Dotted footmen (*P. muscerda)* models and the predation of the Elephant hawk moth (*D. elpenor)* models, controlling for humidity, wind speed, temperature and total precipitation. Wind direction has been removed from the controlled variables because not all four wind directions were present in both subsets of the data.

4. Results

4.1 Survival probability plots

The first probability plot is the average survival probability per proximity to the water (Plot 1). Wherein proximity one is closest to the waterbody and proximity three is furthest away from the waterbody. The plot shows a lower survival probability for proximity one, compared to proximity two and three, which are similar. The second probability plot is the survival probability per treatment (Plot 2), wherein the treatment = reflective are the moth models with the UV marker and treatment = normal are the moth models without the UV marker. This plot shows that the survival probability is on average higher for the moth models with the treatment = normal compared to the moth models with treatment = reflective.



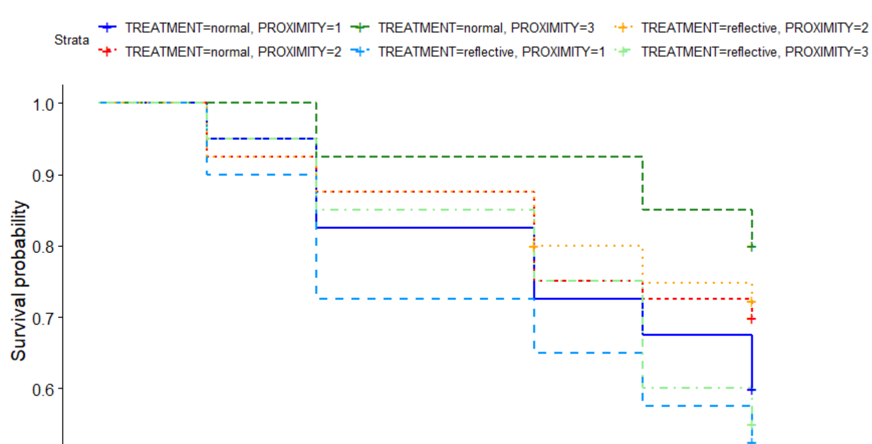


Plot 1: Survival probability per proximity

Plot 2: Survival probability per treatment

The third probability plot is the survival probability per proximity per treatment (Plot 3). For proximity one, the dark blue line is treatment = normal and the light blue line is treatment = reflective. The survival probability for treatment = normal is higher than of treatment = reflective. Indicating that at proximity one, treatment = reflective has an increasing risk of being predated compared to treatment = normal. For proximity two, the red line is treatment = normal and the orange line is treatment = reflective. The survival probability for treatment = normal is lower than of treatment = reflective. Indicating that at proximity two, treatment = reflective has a decreased risk of being predated compared to treatment = normal.

For proximity three, the dark green line is treatment = normal and the light green line is treatment = reflective. The survival probability of treatment = normal is higher than of treatment = reflective. Indicating that at proximity three, treatment = reflective has an increased risk of being predated compared to treatment = normal.



Plot 3: Survival probability per treatment per proximity

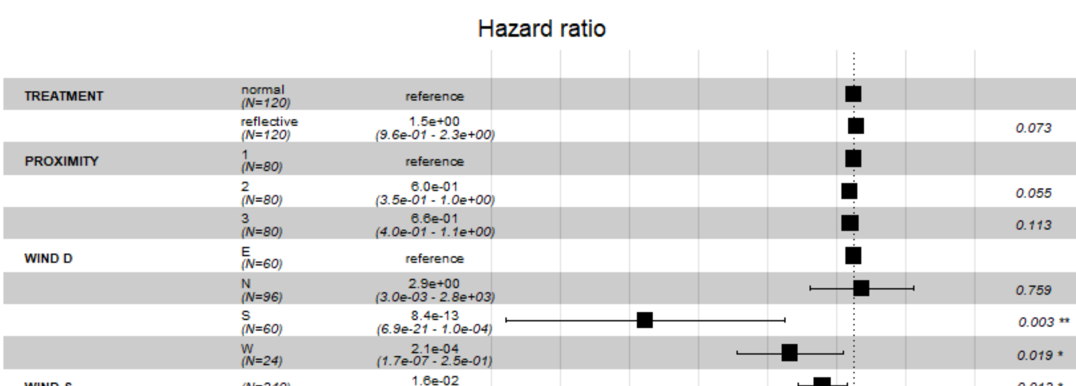
4.2 Cox's Proportional hazard model

4.2.1. Variables individually

For the first model, the effect of nine variables on the survival time of the moth models was analysed (Table 1, Plot 4). The variables contained: proximity, treatment (normal / reflective), wind direction, wind speed, temperature, total precipitation, site and model species. The wind direction South (p = 0.003) and West (p = 0.019), increasing wind speed (p = 0.013) and model species Dotted footmen (p = 0.004) compared to their respective reference values all significantly decreased the risk of being predated. Increasing precipitation (p = 0.019) at site Friesland (p = 0.005) and Groningen (p = 0.003) compared to their respective reference values all significantly increased the risk of being predated.

```
Call:
coxph(formula = Surv(TIME, PREDATED) ~ TREATMENT + PROXIMITY +
    `WIND D` + `WIND S` + HUMIDITY + TEMPERATURE + PRECIPITATION +
    PROVINCE + COLOR)

  n= 240, number of events= 84

                          coef  exp(coef)   se(coef)      z Pr(>|z|)
TREATMENTreflective  3.965e-01  1.487e+00  2.211e-01  1.793  0.07290 .
PROXIMITY2          -5.068e-01  6.024e-01  2.721e-01 -1.863  0.06247 .
PROXIMITY3          -3.542e-01  7.017e-01  3.399e-01 -1.042  0.29736
`WIND D`N            1.111e+00  3.037e+00  3.578e+00  0.310  0.75620
`WIND D`S           -2.680e+01  2.298e-12  9.957e+00 -2.691  0.00711 **
`WIND D`W           -8.120e+00  2.975e-04  3.842e+00 -2.113  0.03457 *
`WIND S`            -3.940e+00  1.944e-02  1.756e+00 -2.243  0.02487 *
HUMIDITY            -3.379e-02  9.668e-01  1.271e-01 -0.266  0.79039
TEMPERATURE          8.057e-01  2.238e+00  1.226e+00  0.657  0.51119
PRECIPITATION        2.131e-01  1.238e+00  1.085e-01  1.965  0.04946 *
PROVINCEFriesland    1.173e+01  1.239e+05  4.577e+00  2.562  0.01040 *
PROVINCEGroningen    7.831e+00  2.517e+03  2.873e+00  2.726  0.00641 **
COLORwhite          -2.433e+01  2.711e-11  8.978e+00 -2.710  0.00673 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

                    exp(coef) exp(-coef) lower .95 upper .95
TREATMENTreflective 1.487e+00  6.727e-01 9.639e-01 2.293e+00
PROXIMITY2          6.024e-01  1.660e+00 3.534e-01 1.027e+00
PROXIMITY3          7.017e-01  1.425e+00 3.604e-01 1.366e+00
`WIND D`N           3.037e+00  3.292e-01 2.733e-03 3.375e+03
`WIND D`S           2.298e-12  4.352e+11 7.691e-21 6.866e-04
`WIND D`W           2.975e-04  3.361e+03 1.596e-07 5.546e-01
`WIND S`            1.944e-02  5.144e+01 6.217e-04 6.078e-01
HUMIDITY            9.668e-01  1.034e+00 7.536e-01 1.240e+00
TEMPERATURE         2.238e+00  4.468e-01 2.023e-01 2.477e+01
PRECIPITATION       1.238e+00  8.081e-01 1.000e+00 1.531e+00
PROVINCEFriesland   1.239e+05  8.069e-06 1.575e+01 9.752e+08
PROVINCEGroningen   2.517e+03  3.973e-04 9.032e+00 7.015e+05
COLORwhite          2.711e-11  3.689e+10 6.181e-19 1.189e-03

Concordance= 0.693  (se = 0.028 )
Likelihood ratio test= 41.6  on 13 df,   p=8e-05
Wald test            = 27.51  on 13 df,   p=0.01
Score (logrank) test = 34.88  on 13 df,   p=9e-04
```

Table 1: The coefficients and p values for the nine measured variables from the cox proportional hazard model



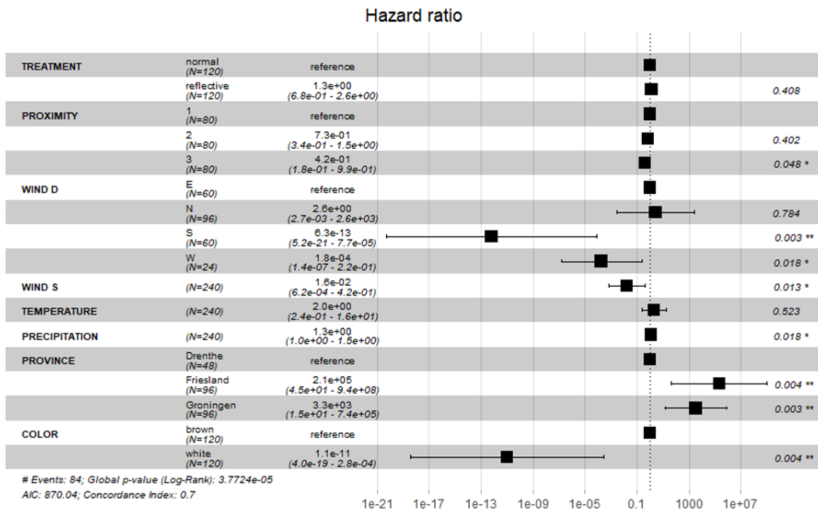
Plot 4: The hazard ratio's and p values for the nine measured variables from the cox proportional hazard model

4.2.2. Treatment per proximity

For the second analysis (Table 2, Plot 5), the effect of treatment on predation per proximity, the likelihood-ratio test, Wald test and score (logrank) test were all statistically significant ($p = 0.00004$, $p = 0.008$ and $p = 0.0006$ respectively) . Therefore, we can reject the null hypothesis that none of the variables that were investigated had an effect on the survival time. The model that was created fits 70,1% of the data that was collected, since the concordance was 0,701. This is higher than the 50% that is expected when the data is totally random.Results from the analysis show that the moth models at proximity three were statistically significantly less likely to be predated than the moth models at proximity one ($p = 0.04765$). No statistically significant difference was observed between the two treatments and the proximities.The weather variables that were controlled for did show statistical significance. The wind speed ($p = 0.01302$) and wind direction South ($p = 0.00310$) and West ($p = 0.01757$) decreased the likelihood of predation, while the wind direction North ($p = 0.078361$) did not show any statistical significant effect on predation, compared to their respective reference value East. Additionally, the total precipitation ($p = 0.01782$) increased the likelihood of predation. Furthermore, the *P. muscerda* species models were less likely to be predated than the *D. elpenor* species models ($p = 0.00377$). Lastly, the moth models at the site in Drenthe were less likely to be predated than the moth models at the sites in Friesland ($p = 0.0044$) and Groningen ($p = 0.00328$).

```
Call:
coxph(formula = Surv(TIME, PREDATED) ~ TREATMENT * PROXIMITY +
    `WIND D` + `WIND S` + TEMPERATURE + PRECIPITATION + PROVINCE +
    COLOR)

  n= 240, number of events= 84

                                   coef  exp(coef)   se(coef)      z Pr(>|z|)
TREATMENTreflective           2.817e-01  1.325e+00  3.405e-01  0.827  0.40811
PROXIMITY2                   -3.212e-01  7.253e-01  3.831e-01 -0.838  0.40180
PROXIMITY3                   -8.595e-01  4.234e-01  4.340e-01 -1.980  0.04765 *
`WIND D`N                     9.649e-01  2.625e+00  3.514e+00  0.275  0.78361
`WIND D`S                    -2.809e+01  6.313e-13  9.498e+00 -2.958  0.00310 **
`WIND D`W                    -8.628e+00  1.791e-04  3.633e+00 -2.375  0.01757 *
`WIND S`                     -4.123e+00  1.619e-02  1.661e+00 -2.483  0.01302 *
TEMPERATURE                   6.841e-01  1.982e+00  1.070e+00  0.639  0.52256
PRECIPITATION                 2.300e-01  1.259e+00  9.706e-02  2.369  0.01782 *
PROVINCEFriesland             1.224e+01  2.073e+05  4.298e+00  2.848  0.00440 **
PROVINCEGroningen             8.108e+00  3.322e+03  2.758e+00  2.940  0.00328 **
COLORwhite                   -2.527e+01  1.064e-11  8.721e+00 -2.897  0.00377 **
TREATMENTreflective:PROXIMITY2 -3.663e-01  6.933e-01  5.394e-01 -0.679  0.49712
TREATMENTreflective:PROXIMITY3  7.314e-01  2.078e+00  5.449e-01  1.342  0.17953
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

                               exp(coef) exp(-coef) lower .95 upper .95
TREATMENTreflective            1.325e+00  7.545e-01 6.800e-01 2.583e+00
PROXIMITY2                     7.253e-01  1.379e+00 3.423e-01 1.537e+00
PROXIMITY3                     4.234e-01  2.362e+00 1.808e-01 9.911e-01
`WIND D`N                      2.625e+00  3.810e-01 2.680e-03 2.570e+03
`WIND D`S                      6.313e-13  1.584e+12 5.192e-21 7.675e-05
`WIND D`W                      1.791e-04  5.583e+03 1.447e-07 2.217e-01
`WIND S`                       1.619e-02  6.177e+01 6.249e-04 4.194e-01
TEMPERATURE                    1.982e+00  5.046e-01 2.435e-01 1.614e+01
PRECIPITATION                  1.259e+00  7.946e-01 1.041e+00 1.522e+00
PROVINCEFriesland              2.073e+05  4.825e-06 4.550e+01 9.443e+08
PROVINCEGroningen              3.322e+03  3.011e-04 1.492e+01 7.393e+05
COLORwhite                     1.064e-11  9.397e+10 4.015e-19 2.820e-04
TREATMENTreflective:PROXIMITY2 6.933e-01  1.442e+00 2.409e-01 1.996e+00
TREATMENTreflective:PROXIMITY3 2.078e+00  4.812e-01 7.142e-01 6.046e+00

Concordance= 0.701  (se = 0.027 )
Likelihood ratio test= 45.21  on 14 df,   p=4e-05
Wald test            = 29.84  on 14 df,   p=0.008
Score (logrank) test = 37.78  on 14 df,   p=6e-04
```

Table 2: The coefficients and p values for the interaction between treatment and proximities and the six control variables from the cox proportional hazard model



Plot 5: The hazard ratio's and p values for treatment and proximity and the six control variables from the cox proportional hazard model

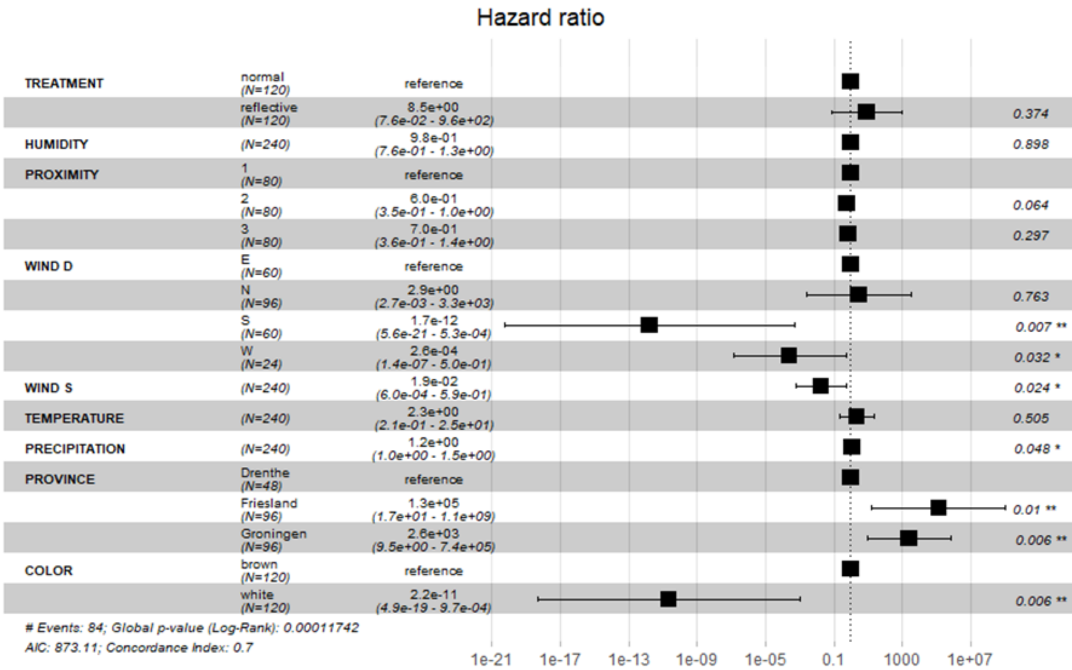
4.2.3 Treatment per humidity

The third analysis (Table 3, Plot 6), the effect of treatment on predation per average humidity, was again statistically significant for the likelihood-ratio test, Wald test and score (logrank) test (p = 0.0004, p = 0.02 and p = 0.002 respectively). Therefore, again the null hypothesis can be rejected. The concordance was in this analysis slightly lower than in the first analysis, namely 0.696, but still high enough to rule out random data. The effect of average humidity per proximity did not show any statistical significance (p = 0.89783). The controlling variables wind direction South (p = 0.00659) and West (p = 0.03220) and wind speed (p = 0.06382) again decreased the risk of predation. While total precipitation (p = 0.04783) also in this model, increased the risk of predation. The sites in Friesland (p = 0.00987) and Groningen (p = 0.00610) had an increased risk of predation compared to their respective reference value site Drenthe. Additionally, in this model the *P. muscerda* models were less likely to be predated compared to the models of *D. elpenor* (p = 0.00629)

```
Call:
coxph(formula = Surv(TIME, PREDATED) ~ TREATMENT * HUMIDITY +
    `WIND D` + `WIND S` + PROXIMITY + TEMPERATURE + PRECIPITATION +
    PROVINCE + COLOR)

  n= 240, number of events= 84

                                 coef  exp(coef)   se(coef)      z Pr(>|z|)
TREATMENTreflective         2.143e+00  8.522e+00  2.411e+00  0.889  0.37412
HUMIDITY                   -1.661e-02  9.835e-01  1.294e-01 -0.128  0.89783
`WIND D`N                   1.079e+00  2.941e+00  3.576e+00  0.302  0.76290
`WIND D`S                  -2.709e+01  1.726e-12  9.970e+00 -2.717  0.00659 **
`WIND D`W                  -8.241e+00  2.636e-04  3.848e+00 -2.142  0.03220 *
`WIND S`                   -3.969e+00  1.890e-02  1.756e+00 -2.260  0.02383 *
PROXIMITY2                 -5.044e-01  6.039e-01  2.722e-01 -1.853  0.06382 .
PROXIMITY3                 -3.542e-01  7.018e-01  3.398e-01 -1.042  0.29734
TEMPERATURE                 8.168e-01  2.263e+00  1.225e+00  0.667  0.50494
PRECIPITATION               2.148e-01  1.240e+00  1.085e-01  1.979  0.04783 *
PROVINCEFriesland           1.181e+01  1.347e+05  4.578e+00  2.580  0.00987 **
PROVINCEGroningen           7.878e+00  2.639e+03  2.873e+00  2.743  0.00610 **
COLORwhite                 -2.454e+01  2.190e-11  8.983e+00 -2.732  0.00629 **
TREATMENTreflective:HUMIDITY -2.664e-02  9.737e-01  3.658e-02 -0.728  0.46640
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
                             exp(coef) exp(-coef) lower .95 upper .95
TREATMENTreflective          8.522e+00  1.173e-01 7.560e-02 9.606e+02
HUMIDITY                     9.835e-01  1.017e+00 7.633e-01 1.267e+00
`WIND D`N                    2.941e+00  3.400e-01 2.657e-03 3.257e+03
`WIND D`S                    1.726e-12  5.794e+11 5.632e-21 5.289e-04
`WIND D`W                    2.636e-04  3.794e+03 1.399e-07 4.966e-01
`WIND S`                     1.890e-02  5.291e+01 6.049e-04 5.905e-01
PROXIMITY2                   6.039e-01  1.656e+00 3.542e-01 1.029e+00
PROXIMITY3                   7.018e-01  1.425e+00 3.605e-01 1.366e+00
TEMPERATURE                  2.263e+00  4.419e-01 2.051e-01 2.497e+01
PRECIPITATION                1.240e+00  8.067e-01 1.002e+00 1.533e+00
PROVINCEFriesland            1.347e+05  7.422e-06 1.710e+01 1.061e+09
PROVINCEGroningen            2.639e+03  3.789e-04 9.470e+00 7.356e+05
COLORwhite                   2.190e-11  4.567e+10 4.939e-19 9.708e-04
TREATMENTreflective:HUMIDITY 9.737e-01  1.027e+00 9.063e-01 1.046e+00

Concordance= 0.696  (se = 0.028 )
Likelihood ratio test= 42.14  on 14 df,   p=1e-04
Wald test            = 27.4  on 14 df,   p=0.02
Score (logrank) test = 34.88  on 14 df,   p=0.002
```

Table 3: The coefficients and p values for the interaction between treatment and humidity and the seven control variables from the cox proportional hazard model



Plot 6: The hazard ratio's and p values for treatment and humidity and the seven control variables from the cox proportional hazard model

4.2.4 Treatment per proximity per species

The fourth analysis (Table 4), the effect of the treatment on predation per species per proximity, gave statistical significance for the likelihood-ratio test, Wald test and score (logrank) test (p = 0.0002, p = 0.02 and p = 0.001 respectively) . Once more the null hypothesis can be rejected. The main item that stands out in this model is the effect the ultraviolet treatment has at proximity two and three for the *P. muscerda* species models. It is respectively 7.747 (p = 0.06612) and 5.690 (p = 0.12090) times as high as for the *D. elpenor* species models. However, these values were not statistically significant.

```
Call:
coxph(formula = Surv(TIME, PREDATED) ~ TREATMENT * PROXIMITY *
    COLOR + HUMIDITY + `WIND D` + `WIND S` + TEMPERATURE + PRECIPITATION +
    PROVINCE)

  n= 240, number of events= 84

                                            coef  exp(coef)   se(coef)      z Pr(>|z|)
TREATMENTreflective                    6.812e-01  1.976e+00  4.518e-01  1.508  0.13157
PROXIMITY2                             6.802e-02  1.070e+00  5.045e-01  0.135  0.89274
PROXIMITY3                            -5.700e-01  5.655e-01  6.434e-01 -0.886  0.37566
COLORwhite                            -2.472e+01  1.844e-11  9.276e+00 -2.665  0.00771 **
HUMIDITY                              -2.936e-03  9.971e-01  1.334e-01 -0.022  0.98245
`WIND D`N                              9.312e-01  2.538e+00  3.506e+00  0.266  0.79054
`WIND D`S                             -2.789e+01  7.754e-13  1.031e+01 -2.706  0.00681 **
`WIND D`W                             -8.586e+00  1.868e-04  3.914e+00 -2.193  0.02828 *
`WIND S`                              -4.083e+00  1.685e-02  1.793e+00 -2.277  0.02279 *
TEMPERATURE                            7.005e-01  2.015e+00  1.225e+00  0.572  0.56745
PRECIPITATION                          2.280e-01  1.256e+00  1.123e-01  2.031  0.04227 *
PROVINCEFriesland                      1.211e+01  1.812e+05  4.692e+00  2.580  0.00987 **
PROVINCEGroningen                      8.040e+00  3.103e+03  2.931e+00  2.743  0.00609 **
TREATMENTreflective:PROXIMITY2        -1.240e+00  2.893e-01  7.280e-01 -1.704  0.08842 .
TREATMENTreflective:PROXIMITY3        -2.369e-02  9.766e-01  7.269e-01 -0.033  0.97400
TREATMENTreflective:COLORwhite        -9.656e-01  3.808e-01  7.047e-01 -1.370  0.17061
PROXIMITY2:COLORwhite                 -9.175e-01  3.995e-01  7.937e-01 -1.156  0.24770
PROXIMITY3:COLORwhite                 -6.564e-01  5.187e-01  8.980e-01 -0.731  0.46480
TREATMENTreflective:PROXIMITY2:COLORwhite  2.047e+00  7.747e+00  1.114e+00  1.838  0.06612 .
TREATMENTreflective:PROXIMITY3:COLORwhite  1.739e+00  5.690e+00  1.121e+00  1.551  0.12090
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

                                          exp(coef) exp(-coef) lower .95 upper .95
TREATMENTreflective                       1.976e+00  5.060e-01 8.153e-01 4.790e+00
PROXIMITY2                                1.070e+00  9.342e-01 3.982e-01 2.877e+00
PROXIMITY3                                5.655e-01  1.768e+00 1.602e-01 1.996e+00
COLORwhite                                1.844e-11  5.424e+10 2.346e-19 1.449e-03
HUMIDITY                                  9.971e-01  1.003e+00 7.676e-01 1.295e+00
`WIND D`N                                 2.538e+00  3.941e-01 2.632e-03 2.447e+03
`WIND D`S                                 7.754e-13  1.290e+12 1.312e-21 4.583e-04
`WIND D`W                                 1.868e-04  5.354e+03 8.699e-08 4.010e-01
`WIND S`                                  1.685e-02  5.933e+01 5.015e-04 5.664e-01
TEMPERATURE                               2.015e+00  4.963e-01 1.826e-01 2.223e+01
PRECIPITATION                             1.256e+00  7.961e-01 1.008e+00 1.565e+00
PROVINCEFriesland                         1.812e+05  5.518e-06 1.838e+01 1.787e+09
PROVINCEGroningen                         3.103e+03  3.223e-04 9.920e+00 9.707e+05
TREATMENTreflective:PROXIMITY2            2.893e-01  3.457e+00 6.945e-02 1.205e+00
TREATMENTreflective:PROXIMITY3            9.766e-01  1.024e+00 2.350e-01 4.059e+00
TREATMENTreflective:COLORwhite            3.808e-01  2.626e+00 9.568e-02 1.515e+00
PROXIMITY2:COLORwhite                     3.995e-01  2.503e+00 8.432e-02 1.893e+00
PROXIMITY3:COLORwhite                     5.187e-01  1.928e+00 8.924e-02 3.015e+00
TREATMENTreflective:PROXIMITY2:COLORwhite 7.747e+00  1.291e-01 8.726e-01 6.878e+01
TREATMENTreflective:PROXIMITY3:COLORwhite 5.690e+00  1.757e-01 6.323e-01 5.121e+01
```

Table 4: The coefficients and p values for the interaction between treatment, proximity and color and the six control variables from the cox proportional hazard model

4.2.5. Treatment per proximity for each species

The fifth analysis (Table 5, Table 6), the effect of treatment on predation per species, consisted of two models, each for every species. For *P. muscerda* the data fit into the model for 77,2% and also for this analysis the likelihood-ratio test, Wald test and score (logrank) test all were statistically significant (p = 0.0002, p = 0.02 and p = 0.0004 respectively). So, the null hypothesis that none of the investigated variables had an effect on the survival time can be rejected. This analysis showed that at proximity one the Dotted footmen models were less likely to be predated than at proximity three (p = 0.0364). Adding to that, the ultraviolet treatment has an increasing effect on the predation at proximity three compared to proximity one (p = 0.0452). Meaning that the risk for UV treated models was 5.54 times higher than for the non UV treated models at proximity three compared to proximity one. For the *D. elpenor* analysis, the data fit into the model for 67,3%. No statistical significance was shown by the likelihood-ratio test, Wald test or score (logrank) test (p = 0.2, p = 0.3 and p = 0.2 respectively). Therefore, the null hypothesis that none of the investigated variables had an effect on the survival time can not be rejected.

```
Call:
coxph(formula = Surv(TIME, PREDATED) ~ TREATMENT * PROXIMITY +
    `WIND S` + HUMIDITY + TEMPERATURE + PRECIPITATION + PROVINCE,
    data = data_white)

  n= 120, number of events= 37

                                coef exp(coef) se(coef)      z Pr(>|z|)
TREATMENTreflective         -0.27649   0.75844  0.54068 -0.511   0.6091
PROXIMITY2                  -0.88029   0.41466  0.61374 -1.434   0.1515
PROXIMITY3                  -1.82134   0.16181  0.87040 -2.093   0.0364 *
`WIND S`                    -0.25735   0.77310  4.57909 -0.056   0.9552
HUMIDITY                     0.50057   1.64966  0.43539  1.150   0.2503
TEMPERATURE                 -3.75994   0.02329  4.34152 -0.866   0.3865
PRECIPITATION                0.63222   1.88178  0.46632  1.356   0.1752
PROVINCEFriesland            1.06938   2.91358 14.19692  0.075   0.9400
PROVINCEGroningen            2.95006  19.10711  6.95606  0.424   0.6715
TREATMENTreflective:PROXIMITY2  0.78092   2.18348  0.84296  0.926   0.3542
TREATMENTreflective:PROXIMITY3  1.71210   5.54061  0.85501  2.002   0.0452 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

                               exp(coef) exp(-coef) lower .95 upper .95
TREATMENTreflective              0.75844    1.31850 2.628e-01 2.189e+00
PROXIMITY2                       0.41466    2.41161 1.245e-01 1.381e+00
PROXIMITY3                       0.16181    6.18016 2.938e-02 8.910e-01
`WIND S`                         0.77310    1.29350 9.784e-05 6.109e+03
HUMIDITY                         1.64966    0.60618 7.027e-01 3.873e+00
TEMPERATURE                      0.02329   42.94575 4.694e-06 1.155e+02
PRECIPITATION                    1.88178    0.53141 7.545e-01 4.694e+00
PROVINCEFriesland                2.91358    0.34322 2.399e-12 3.539e+12
PROVINCEGroningen               19.10711    0.05234 2.292e-05 1.593e+07
TREATMENTreflective:PROXIMITY2   2.18348    0.45798 4.184e-01 1.139e+01
TREATMENTreflective:PROXIMITY3   5.54061    0.18049 1.037e+00 2.960e+01

Concordance= 0.772  (se = 0.033 )
Likelihood ratio test= 36.2  on 11 df,   p=2e-04
Wald test            = 22.48  on 11 df,   p=0.02
Score (logrank) test = 31.65  on 11 df,   p=9e-04
```

Tabel 5: The coefficients and p values for the interaction between treatment and proximity and the five control variables of only the white models from the cox proportional hazard model

```
Call:
coxph(formula = Surv(TIME, PREDATED) ~ TREATMENT * PROXIMITY +
    `WIND S` + HUMIDITY + TEMPERATURE + PRECIPITATION + PROVINCE,
    data = data_brown)

  n= 120, number of events= 47

                                  coef exp(coef) se(coef)      z Pr(>|z|)
TREATMENTreflective             0.7164    2.0471   0.4543  1.577   0.1148
PROXIMITY2                      0.2038    1.2261   0.5197  0.392   0.6949
PROXIMITY3                      0.1089    1.1151   0.9261  0.118   0.9064
`WIND S`                        0.3525    1.4226   0.5539  0.636   0.5246
HUMIDITY                       -0.3103    0.7332   0.3241 -0.957   0.3383
TEMPERATURE                     1.8991    6.6802   1.9729  0.963   0.3357
PRECIPITATION                  -0.1615    0.8508   0.3789 -0.426   0.6699
PROVINCEFriesland              -0.3732    0.6885   1.7859 -0.209   0.8345
PROVINCEGroningen               0.9362    2.5503   1.1974  0.782   0.4343
TREATMENTreflective:PROXIMITY2 -1.2923    0.2747   0.7301 -1.770   0.0767 .
TREATMENTreflective:PROXIMITY3 -0.0536    0.9478   0.7289 -0.074   0.9414
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

                               exp(coef) exp(-coef) lower .95 upper .95
TREATMENTreflective               2.0471     0.4885   0.84022     4.987
PROXIMITY2                        1.2260     0.8156   0.44275     3.395
PROXIMITY3                        1.1151     0.8968   0.18155     6.849
`WIND S`                          1.4226     0.7029   0.48036     4.213
HUMIDITY                          0.7332     1.3638   0.38850     1.384
TEMPERATURE                       6.6802     0.1497   0.13977   319.271
PRECIPITATION                     0.8508     1.1753   0.40485     1.788
PROVINCEFriesland                 0.6885     1.4524   0.02079    22.806
PROVINCEGroningen                 2.5503     0.3921   0.24398    26.658
TREATMENTreflective:PROXIMITY2    0.2746     3.6410   0.06566     1.149
TREATMENTreflective:PROXIMITY3    0.9478     1.0551   0.22714     3.955

Concordance= 0.673  (se = 0.037 )
Likelihood ratio test= 14.41  on 11 df,   p=0.2
Wald test            = 13.46  on 11 df,   p=0.3
Score (logrank) test = 14.94  on 11 df,   p=0.2
```

Tabel 6: The coefficients and p values for the interaction between treatment and proximity and the five control variables of only the brown models from the cox proportional hazard model

5. Discussion

5.1 Summary

The white species models showed significantly less predation at a 30 meter distance from the waterbody compared to a 0 meter distance and a significantly higher positive effect of UV treatment on predation at 30 meters than at 0 meters. This would support the hypothesis that UV reflection is indeed beneficial for species living close to water bodies. However, this effect cannot be seen in the models of the brown species. So to answer the question : ”To what degree can ultraviolet reflectance in the wings of nocturnal lepidoptera function as a form of camouflage?”. It depends on the species of moth and their color, as species with a brighter color seem to benefit from the UV reflectance when near bodies of water, while species with dull colors don’t. Difference in location also has a significant effect on the predation, as models within the province of Drenthe were overall less predated compared to the other two provinces.

5.2 Discussion

5.2.1 Locations

The difference in results at the location of Drenthe compared to the other two provinces, might be caused by a boom of caterpillars of the Mottled umber and other species in the oak trees present (“Rupsen eten Drentse bomen kaal”, 2023). A reason for this only affecting drenthe is that the forest mainly consisted of oaks, while the oak density in the other locations was lower up until no oaks at all. Due to this overabundance of prey, chances are that the insectivorous birds predated this already well known prey higher up in the trees, as it is an easy snack. Another factor that could have influenced the results at all locations is that research performed by Atienza en Illera (1997) showed that most insectivorous birds tend to forage higher up in the trees at a minimum height of approximately 3 meters, while the models were hung at a height of 1.6 meters for convenience. Besides this, one can also argue that the tree types that the moths are pinned on influenced the results, as brown models in a brown tree will of course be noticed later than white models on a brown tree. This might be why for the white models a significant difference was seen but for brown models there was not. Locations could also have been influenced, in particular recreation, as the location in Drenthe had a pathway that was fairly popular among dog walkers and the location in Friesland had a preschool excursion present at their site. This could have influenced the results as the dogs and loud children tend to scare away birds, making them forage somewhere else. This could have been prevented by creating a disturbance scale and control for it in the models, yet this was not done due to time constraints.

5.2.2 Precipitation

Besides this, the birds were not the only organisms preying on the models. On days with lots of precipitation, it was observed that species like Common rough woodlouse (*Porcellio scaber*), Garden slug (*Arion hortensis*) and Common red ant (*Myrmica rubra*) either predated on the mealworms present on the model or destroyed the model itself. Even Though upon observing this the models were replaced, this could have influenced the results as before replacing it a bird could have predated it, if it was not already destroyed.Furthermore, rainfall caused the UV ink to wear off or alter in color, resulting in birds not being able to see the difference or a model that lost its UV effect being counted as one treated with UV ink. The destruction of models by rain and woodlouse could have been prevented by wrapping models into foil. However, the effect of this foil on the UV reflectance of these models was not known and thus it was decided not to use this.

5.2.3 Weather conditions

Rainfall was not the only weather condition influencing the results. Another point of attention is that the humidity gradient that was expected, being the highest around the water and lower when further away, was not present in this form. What was measured was a reversed humidity gradient at which the humidity was highest at proximity 3 and lowest at proximity 1, for all 3 provinces. This could have been caused by the rainy weather. Another factor that could have influenced these results is the wind. As areas around water bodies are generally more open and thus let more wind through, dry air could have been brought in by the wind resulting in lower values. However in an attempt to prevent this, the device was placed out of the wind at the height of the hip, using the body as a sort of windshield. In addition every measurement the device was left to calibrate until the values stabilized, resulting in more accurate and trustworthy results.

5.2.4 Conclusion

For future research it is of interest to repeat this experiment in a controlled environment, so other factors such as wind and temperature can have as little influence on the results as possible. This way it can be determined if it was really the influence of humidity or that other factors might also have played a role in this. Furthermore, other species of animals could also be researched to determine if this way of camouflage is specific for lepidoptera or if other organisms might take advantage of it too, as this way of camouflage has also already been hypothesized by Suárez-Tovar et al. (2022) to be present within certain dragonfly species. But also within lepidoptera, to test if the UV reflectance is just limited to the imago of the butterfly or if the caterpillar uses a similar type of mechanism. Lastly, if the research is repeated a disturbance scale should be created and controlled for in the models, to rule out any influence from this. To conclude, it is likely that brighter coloured species can benefit from having ultraviolet reflection in their wings. However for the brown variants this cannot be said as the results were insignificant.

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7. Appendix

7.1 Tables of environmental observations

7.1.1 Table 1 - Bird Species

Species	**Common name**	**province**
Parus major	Great tit	Drenthe, Groningen, Friesland
Parus coereleus	Blue tit	Drenthe, Groningen,
Troglodytes troglodytes	Wren	Drenthe, Groningen, Friesland
Dendrocopos major	Great spotted woodpecker	Drenthe, Groningen, Friesland
Turdus merula	Black bird	Drenthe, Groningen, Friesland
Corvus monedula	Crow	Groningen, Friesland
Buteo buteo	Common buzzard	Drenthe
Sylvia atricapilla	Black cap	Drenthe, Groningen, Friesland
Erithacus ruhecula	Red robin	Drenthe, Groningen, Friesland
Fringilla coelebs	Common chaffinch	Drenthe, Groningen
Cuculus canorus	Cuckoo	Drenthe, Groningen, Friesland
Garrulus glandarius	Eurasian jay	Groningen, Friesland
Pica pica	Eurasian magpie	Groningen, Friesland
Phylloscopus collybita	Common chiffchaff	Drenthe, Friesland
Columba palumbus	Common wood pigeon	Drenthe, Friesland
Motacilla alba	White wagtail	Drenthe
Picus viridis	Green woodpecker	Drenthe
Gallinula chloropus	Common moorhen	Drenthe, Groningen
Phoenicurus phoenicurus	Common redstart	Drenthe

Bird species observed per location

7.1.2 Table 2 - Tree Species

Species	Common name	Location
Sorbus	Rowan	Groningen
Crataegus	Hawthorn	Drenthe, Groningen
Alnus	Alder	Groningen
Salix	Willow	Groningen
Cornus	Dogwood	Groningen
Tilia	Linden tree	Drenthe
Quercus	Oak	Drenthe
Fagus	Beech	Friesland
Pinus	Pine	Drenthe, Friesland

Tree species used to pin models on

7.1.3 Table 3 - Insect Species

Species	Common name	Location
Isopoda	Isopods	Drenthe, Friesland, Groningen
Myrmica rubra	Common red ant	Groningen
Opiliones	Daddy longlegs	Friesland
Gastropoda	Slug	Drenthe, Friesland

Insect species that predated on the models

7.2 Figures of locations

7.2.1 Drenthe

A

B

C

Figure 1.a,b and c: An impression of the location in Drenthe

7.2.2 Groningen

A

B

C

Figures 2.a,b and c: an impression of the location in Groningen

7.2.3 Friesland

A

B

C

Figures 3.a,b and c: an impression of the location in Friesland

Acknowledgements

This research and paper would not have been possible without the help and advice of professor dr. H.L. Dugdale and E.A. Young. They have both provided expertise and helped guide us along the way.

A special thanks is also in place for mister and misses Stoffer, for providing us with access to their private property. Without this, finding a study site within the province of Drenthe would have been a lot more difficult. Their generosity is appreciated.