Identify the invisible: Has ultraviolet reflectance influence on the predation of moths by avian predators?

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Carlijn van der Weerd, s3646106
Supervisors: Prof. Dr. H. Dugdale & PhD E. Young
Research Project Ecology & Evolution II
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1. Abstract

Since the 1980’s there are two strategies of camouflage for moths, cryptic and disruptive. But besides different wing patterns, moths also exhibit ultraviolet reflectance in their wings. Although research has been done on the effects of ultraviolet reflectance, this mainly focussed on intraspecies communication. In this study the focus lays in the possibility that ultraviolet reflectance in the wings of moth could function as a camouflage strategy. Moth models of the species *Pelosia muscerda* and *Deilephila elpnor* were exposed to avian predators at different proximities, ranging from points close to a waterbody to points further away from a waterbody. Half of the moth models was treated with ultraviolet ink and the other half was left untreated. Results from this study show that predation of *P. muscerda* was decreased at proximities close to the waterbody and increased at proximities further from the waterbody. Moreover, the ultraviolet treatment decreased the predation at proximities close to the waterbody and increased the predation at proximities further from the waterbody. For *D. elpenor* no difference in predation was detected at different proximities or due to the ultraviolet treatment. From these results can be concluded that species with bright colours and high ultraviolet reflectance can benefit from these traits in habitats with also high ultraviolet reflectance.
Keywords: Moth species, camouflage strategy, ultraviolet reflectance

2. *Introduction*

For centuries, the view on camouflage strategies has not changed. Since at least 1980 (Endler, 1984), two strategies of camouflage explained the way animals work to keep detectability from predators low. The first camouflage strategy is cryptic, whereby the goal is to fade away into the background of the surrounding of the animal. By matching its colours and outlines to the background, the animal is decreasing the change of detectability by predators (Schaefer & Stobbe, 2006). The second camouflage strategy is disruptive. By using arbitrary colours of the background and contrasting colours on the extremities of the animal, it is also able to decrease the detectability by predators (Cuthill Innes C. et al., 2005; Kang et al., 2015; Schaefer & Stobbe, 2006; Stevens M. et al., 2006; Webster et al., 2013).

As humans we see this world between the wavelengths of 400 to 700 nm (nanometres) of the light spectrum, which makes us able to see the three main colours (red, blue and green) and everything in between. Some species of the animal kingdom are not limited to these wavelengths. They are able to see close to the ultraviolet part of the light spectrum, which is between 320 and 400 nm (Honkavaara et al., 2002). Since 1995, the effect ultraviolet vision might have in the animal kingdom has become a point of interest (Tovke, 1995). From that moment on, it has become clear that ultraviolet vision indeed has effects in the animal kingdom. It plays an important role in the communication between intraspecies, mainly in the context of sexual preferences. For instance, in the research by Papke et al. (2007) conclusions were taken that the ultraviolet reflectance in butterfly *Colias eurytheme* was more important to mating success than pheromones. Not only in intraspecies communication but also in circadian rhythms, foraging and navigation is ultraviolet vision a vital key in the lives of some animal species (Tovke, 1995).

Although research has been done on the effects of ultraviolet vision and reflectance, not much information is available on the possible effects ultraviolet reflectance has on predation. Mainly insects and crustaceans are the ones in the animal kingdom that possess ultraviolet receptors (Tovke, 1995). Moth species are an order in the insect class that exhibit such ultraviolet reflectance (Cane et al., 2018; Zapletalová et al., 2016). Even though mostly nocturnal moth species as appose of diurnal moth species display ultraviolet reflectance in their wings, it still raises the question whether the ultraviolet reflectance could be a camouflage strategy. Justification for this question lays in the fact that moth species are mainly predated by avian predators, which have ultraviolet vision (Honkavaara et al., 2002). The interspecies communication between moth species and avian predators could be an indication for the influence by ultraviolet vision and reflectance.

Research done by Zapletalová et al. (2016) showed a link between ultraviolet reflectance in the wings of moth species and the humidity of their habitat. They concluded that moth species living in habitats with high humidity usually had high ultraviolet reflectance in their wings. Since waterbodies and moist vegetation create high ultraviolet reflectance (Cezário et al., 2022), it would be beneficial for animals to additionally have high ultraviolet reflectance to lower detection by avian predators. This research was dedicated to investigate whether moth models with ultraviolet ink will have a higher survival rate at proximities close to the waterbody, due to similar amounts of ultraviolet reflectance of the environment. And whether moth models with ultraviolet ink have a lower survival rate at proximities further away from the waterbody, since they will stand out in a surrounding with low ultraviolet reflectance.

3. Materials and methods

3.1. Models

3.1.1 Model species

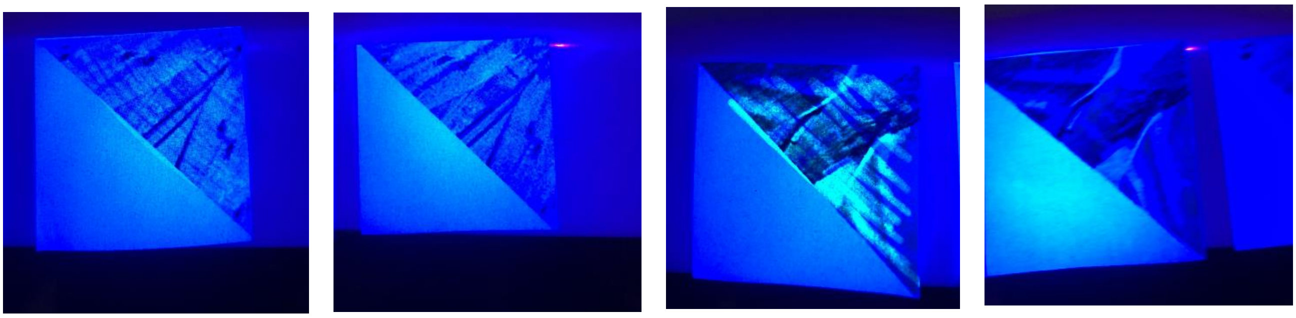
The models for the experiment were created using two moth species, *Deilephila elpenor* (Elephant hawk moth) and *Pelosia muscerda* (Dotted footman). These species were chosen for their difference in habitat and ultraviolet reflectance, as well as their different camouflage strategy. As *P. muscerda* tends to reside in habitats with swamps and water present **(Spitzer & Jaroš, 2010)** and additionally has a high ultraviolet reflectance (Zapletalová et al., 2016), while *D. elpenor* prefers grasslands (e-Vision, The Netherlands, z.d.) and also has a low ultraviolet reflectance (Zapletalová et al., 2016). The Elephant hawk moth additionally resembles the colours of the tree bark (mimic), while the Dotted footman has more disruptive colours.

Elephant hawk, *Deilephila elpenor* (Vlinderstichting.nl)

Dotted footman, *Pelosia muscerda* (Vlinderstichting.nl)

3.1.2 Design

The pattern of their wings was put into a triangle shape, using the program Canva (version 4.64.0), to create a simple moth shape from 62 by 34 mm (height x width). The models were printed on paper and the blank triangle was glued to the back for sturdiness. To create models that will have ultraviolet 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 ultraviolet reflectance. With an ultraviolet light the models were checked whether or not the invisible ink covered the models sufficiently (Figure 1,2,3 & 4). If sufficient enough, the models were left to dry for a night. Two trial runs were performed using the models without ultraviolet treatment at the location in the provinces Drenthe, Friesland and Groningen to ensure birds would predate on these models nonetheless.



1 2 3 4

Figure 1,2,3 and 4: From left to right: Dotted footmen with ultraviolet ink(1), Dotted footmen without ultraviolet ink (2), Elephant hawk moth with ultraviolet ink (3) and Elephant hawk without ultraviolet ink (4)

3.2 Determining location

3.2.1. Orientation

To be able to say anything about the ultraviolet reflectance of the environment, humidity measurement were done. To create a humidity gradient and therefore a ultraviolet 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 is 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 threes 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 be located on the south side of the waterbody, as the sunlight, and thus the ultraviolet 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 are 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 the Black bird (*Turdus merula*), the Great tit (*Parus major*) and the 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 moth models (Appendix, Table 3), and tree species used (Appendix, Table 2), were written down. To give a short description : 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 location, 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 moth 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 of 9th of May and 11th till 12th of May. For these dates, all the trees located at the left of the waterbody had models with ultraviolet ink and all the trees on the right had models without ultraviolet ink. On the 8th of May, at 7:00 the first measurements started with the models of *D. elpenor* and lasted till the 9th of May at 19:00. On the 11th of May the second measurements started at 7:00 with the models of *P. muscerda* and lasted till the 12th of May at 19:00. During the second week of measurements from the 15th to the 16th of May and from the 18th to the 19th of May, the placement of the models was switched, whereby the tress on the left of the waterbody had models without ultraviolet ink and the tress on the right had models with ultraviolet 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 for 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; Siikamaki, 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 brining in air with 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 place 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 of the wind and breathing as much as possible. When values stabilized or after five minutes the results were written down.

3.4 Statistical analysis

For the statistical analysis, the data was 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.

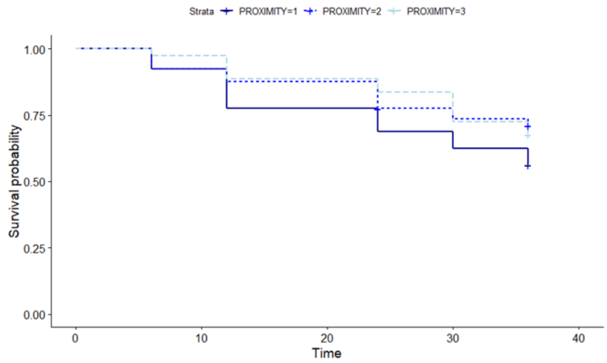
Firstly, the Cox's proportional hazard test was used to test the effect each measured variable had on the predation risk individually, while controlling for all other variables. The variable that were tested were: proximity (to the waterbody), treatment (UV or normal), wind direction, wind speed, temperature, 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 proximity. In this analysis the effect of the UV treatment 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.

The fifth analysis consisted of two models, each for every species. 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

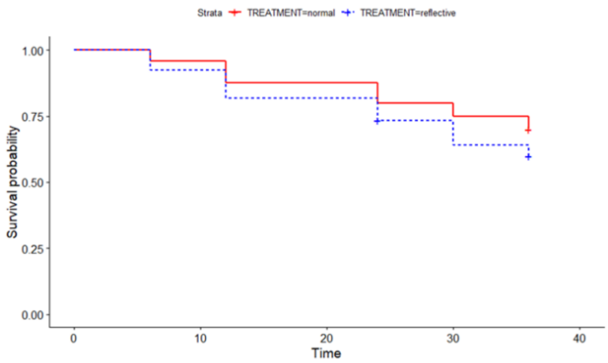
4.1 Survival probability plots

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 to each other.



Plot 1: Survival probability per proximity

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.



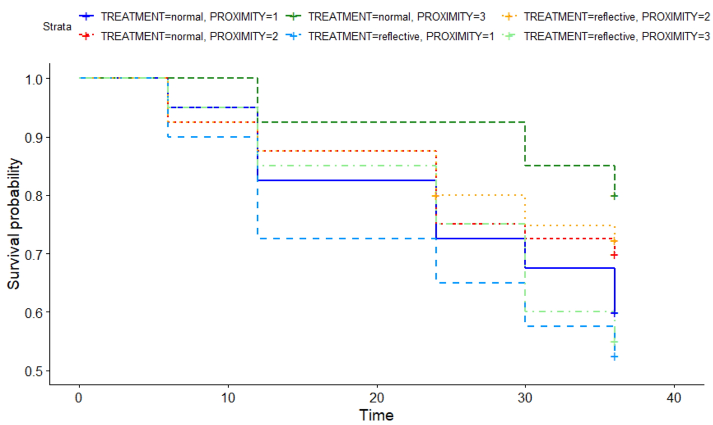
Plot 2: Survival probability per treatment

The third probability plot is the survival probability per proximity per treatment (Plot 3). For proximity one, the dark blue is the treatment = normal and the light blue line is the 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.

4.2 Cox's Proportional Hazard Model

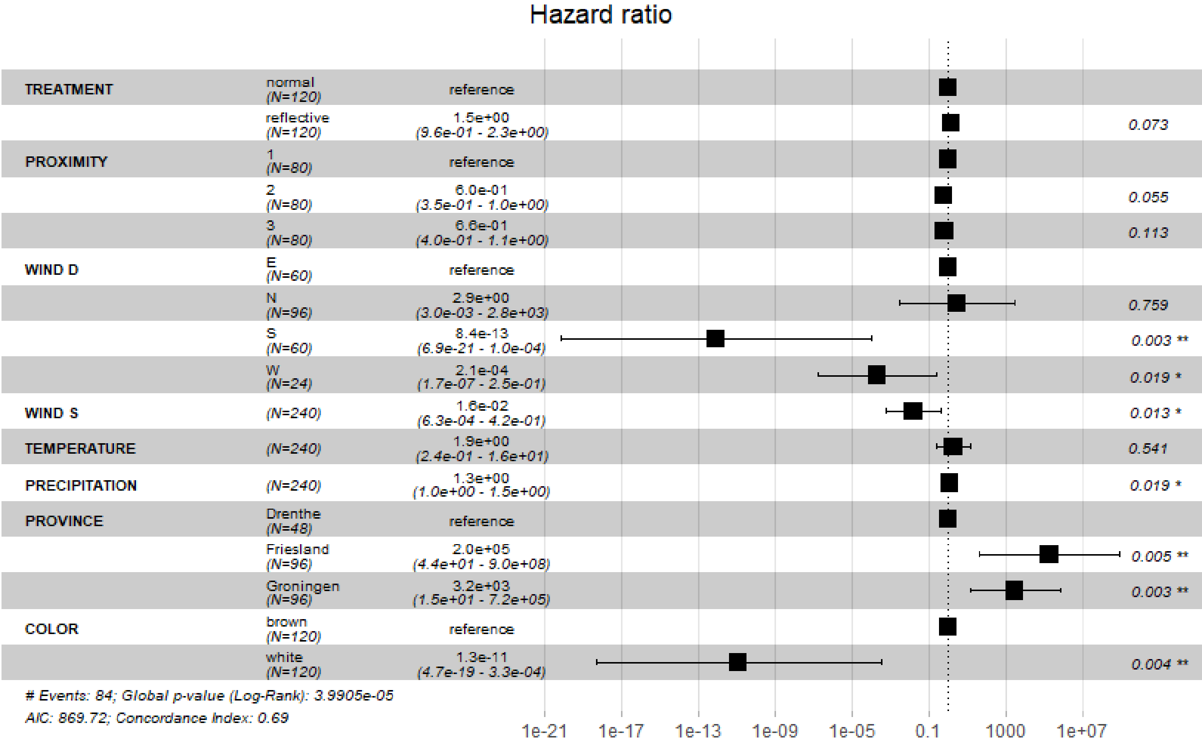
4.2.1. Variables individually

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.



Plot 3: Survival probability per treatment per proximity

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. Increased precipitation ($p = 0.019$) at site Friesland ($p = 0.005$) and Groningen ($p = 0.003$) compared to their respective refence values all significantly increased the risk of being predated.



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

```
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's proportional hazard model

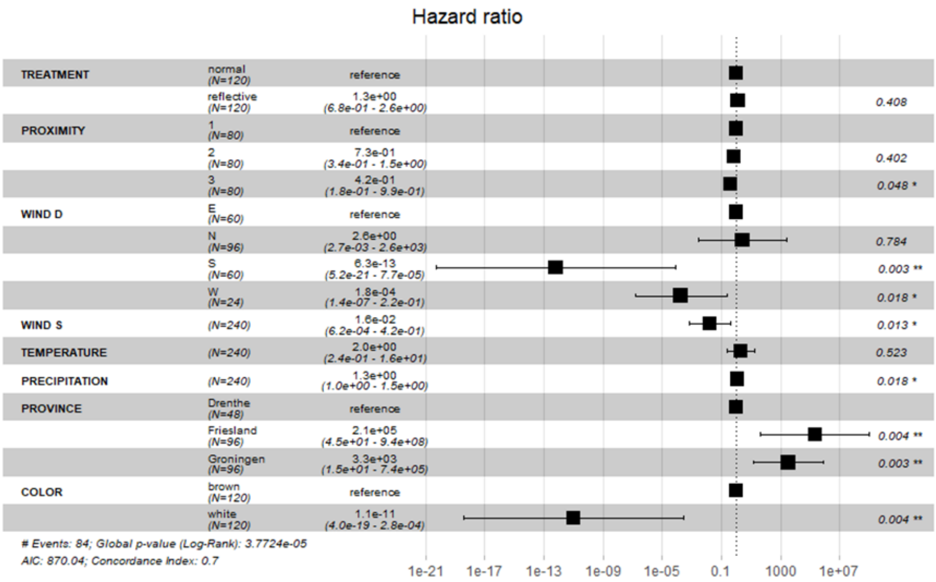
4.2.2. Treatment per proximity

For the second analysis, the effect of treatment on predation per proximity (Table 2, Plot 5), the likelihood-ratio test (p = 0.00004), Wald test (p = 0.008) and score (logrank) test (p = 0.0006) were all statistically significant. Therefore, we can reject the null hypothesis that none of the variables that were investigated has 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.

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 site 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's proportional hazard model



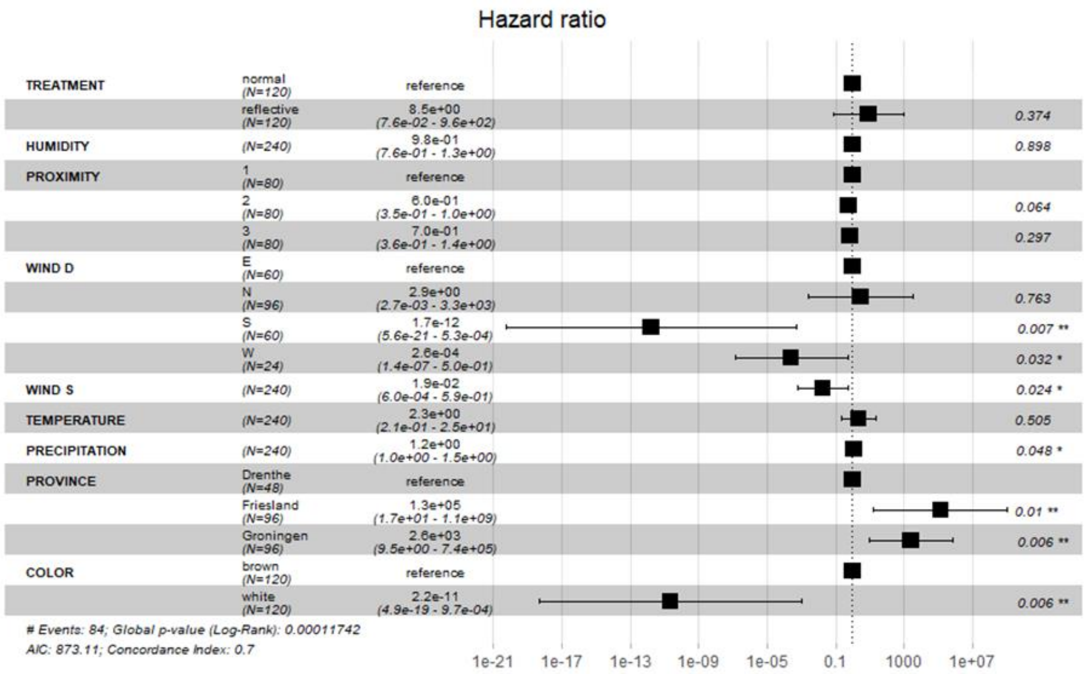
Plot 5: The hazard ratio's and p-values treatment and proximity and the six control variables from the cox's proportional hazard model

4.2.3 Treatment per humidity

The third analysis, the effect of treatment on predation per average humidity (Table 3, Plot 6), was again statistically significant for the likelihood-ratio test (p = 0.0004), Wald test (p = 0.02) and score (logrank) test (p = 0.002). 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 9p = 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’s proportional hazard model



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

4.2.4 Treatment per proximity per species

The fourth analysis, the effect of the treatment on predation per species per proximity (Table 4), gave statistical significance for the likelihood-ratio test (p = 0.0002), Wald test (p = 0.02) and score (logrank) test (p = 0.001). Once more the null hypothesis can be rejected. The main item that stands out in this model is the effect of the UV 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 5: The coefficients and p-values for the interaction between treatment, proximity and species and the six control variables from the cox's proportional hazard model

4.2.5. Treatment per proximity for each species

The fifth analysis, the effect of treatment on predation per species, consisted of two models, for each species one (Table 5 and 6). For *P. muscerda* the data fit into the model for 77.2% and also for this analysis the likelihood-ratio test (p = 0.0002), Wald test (p = 0.02) and score (logrank) test (p = 0.0004) were statistically significant. 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 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 (p = 0.2), Wald test (p = 0.3) and score (logrank) test (p = 0.2). Therefore, the null hypothesis of the investigated variables had an effect 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
```

Table 5: The coefficients and p-values for the interaction between treatment and proximity and the five control variables of *P. muscerda* models from the cox’s 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
```

Table 6: The coefficients and p-values for the interaction between treatment and proximity and the five control variables of *D. elpenor* models from the cox's proportional hazard model

5. Discussion

5.1 Summary

Heterocera is a group of animals with a substantial variety in ultraviolet reflective values in their wings (Cane et al., 2018; Zapletalová et al., 2016). This study showed that depending on the species, ultraviolet reflectance can be a form of camouflage for moths. Although not predicted, there was a difference in the predation risk between the Dotted footmen (*P. muscerda*) and the Elephant hawk moth (*D. elpenor*). The Dotted footmen models were significantly less predated at proximity one, closest to the waterbody, compared to proximity three, furthest away from the waterbody. Additionally, the reflective treatment had a positive effect on the predation risk for the Dotted footmen models. Meaning that at proximities close to the waterbody, the reflective treatment decreased the predation risk. And at proximities furthest away from the waterbody, the reflective treatment increased the predation risk. For the Elephant hawk moth models, no significance difference could be found for the variables that were tested. So, the reflective treatment did not change the predation risk for this species at any proximity. Therefore, only the results from the Dotted footmen supports the hypothesis that ultraviolet reflectance at proximities close to the waterbody are beneficial for lowering predation and that it has a disadvantage for proximities furthest away from the waterbody.

5.2 Discussion

5.2.1 Species

For this study two moth species were chosen based on the paper by Zapleptová et al (2016). The Dotted footmen (*P. muscerda*) has an ultraviolet reflectance value of 47.93 and the Elephant hawk moth (*D. elpenor)* has a value of 14.46. These ultraviolet reflectance values have emerged due to special structures and colours in these moth species(Cezário et al., 2022) . By printing them on paper, only the colour of the moths could create the ultraviolet reflectance. Since no equipment to test the ultraviolet reflectance of the models was not available, the exact ultraviolet reflectance values could not be determined. Additionally, using ultraviolet ink to enhance the ultraviolet reflectance on the wings, might not resemble the ultraviolet reflectance in the wild. Although the results of the study show that the moth species with the highest ultraviolet reflectance value, the Dotted footmen, did benefit at proximities close to the waterbody, does not necessarily indicate that the moth species with the lower ultraviolet reflectance value, the Elephant hawk moth, does not benefit from the lower ultraviolet reflectance in the wild at proximities close to the waterbody.

5.2.2. Humidity

To give an indication of the ultraviolet reflectance of the surroundings of the different proximities, humidity was measured. Since high humidity could imply high ultraviolet reflectance of the surrounding. An humidity gradient going from high at proximities close to the waterbody, to low at proximities furthest away from the waterbody was expected. But in the field a reversed humidity gradient was observed. Due to openness at the proximities close to the waterbody, wind direction and wind speed could have influenced the results from the humidity measurements. Additionally, moisture of the soil and vegetation, which was more abundant at proximities further from the waterbody could have increased the humidity. Due to this reversed humidity gradient, it was decided to do multiple models of the Cox's proportional hazard plots. So, the interaction between humidity and predation was analysed but also the interaction of only the proximity and predation was analysed.

5.2.3. Weather variables & foraging behaviour of birds

When performing this study, weather conditions could not be controlled. Therefore, monitoring and analysing the weather variables was done to control for the effect it might have on the predation of the moth models. Wind direction South and West and increasing wind speed decreased the risk of predation, while precipitation increased the risk of predation. Moreover, the precipitation caused the ultraviolet ink to wear off. This could have influenced the results since a moth with the reflective treatment might not be have the ultraviolet reflectance anymore. Also, the foraging behaviour of the birds could not be controlled. The presence of the bird species Great tit (*Parus major*), Blue tit (*Parus* *coereleus*) and Black bird (*Turdus merula*) were checked for, since these species are insectivorous. But due to mechanical restrictions, it was only possible to pin the models down at a height of 1.60m. While birds tend to forage higher up in the trees (Atienza & Illera, 1997). If the models would have been pinned on the trees at an higher height, the results could have been different.

5.2.4. Further research

Although the database of this study is rather small, it could be a big step into the world of camouflage strategies. The results show that there is a significant effect of the treatment with ultraviolet reflectance. This could indicate that for other species of the animal kingdom, this strategy might also apply. Further research could be done in a more controlling environment, in this way weather variables and bird's foraging behaviour could be accounted for. To get a better understanding in how this strategy exactly works, more research could be done on wing patterns and their ultraviolet reflection and how this effects predation.

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8. Appendix

8.1 Tables of environmental factors

Table 1 Bird species observed per location

Species	Common name	Location
Parus major	Great tit	Drenthe, Groningen, Friesland
Cyanistes 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
Coloumba 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

Table 2 Tree species, which were used to pin moth models on

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 tree	Drenthe
Fagus	Beech tree	Friesland
Pinus	Pine tree	Drenthe, Friesland

Table 3 Insect species, which predated on the moth models

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

8.2 Overview of the locations

8.2.1 Drenthe



A B C

Figure A, B and C: impression of the site at Drenthe

8.2.2. Groningen



D E F

Figure D, E and F: impression of the site at Groningen

8.2.3 Friesland



G H I

Figure G, H and I : impression of the site at Friesland