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Use of time-lapse cameras to monitor beetle activity on fruiting bodies of *Fomitopsis pinicola*

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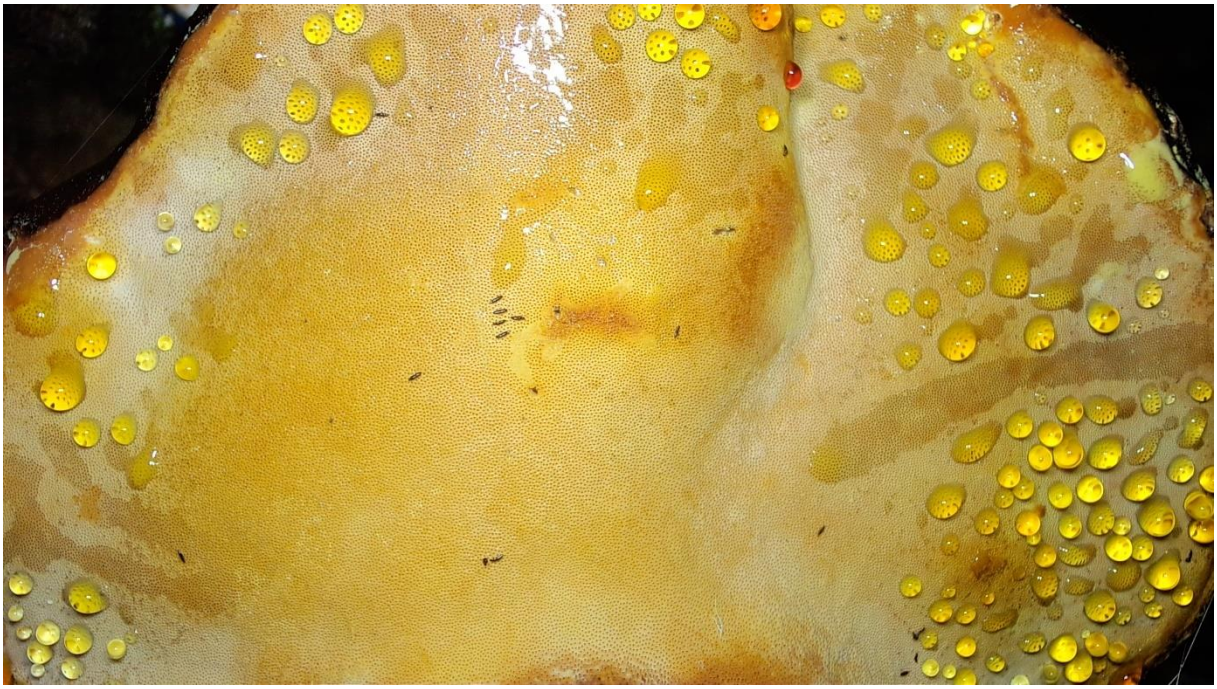

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Preface and Acknowledgements

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Ski, the 17th of August 2020

Bendik J. Ferkingstad

Abstract

Insects and fungi are the major contributors to forest biodiversity. It is apparent that insects have an ecologically important effect on fungal communities in dead wood systems. Beetles frequently visit the fruiting bodies of polypore wood-decay fungi to feed on spores and have the potential to act as targeted dispersal vectors by carrying and disseminating fungal propagules. However, and despite the hypothesised importance of this interaction, we know little of who these beetle visitors are, when and how often they visit, or how long a typical visit lasts.

In this study, beetle activity on fruiting bodies of *Fomitopsis pinicola* (Sw.) P.Karst. was monitored by using commercial time-lapse cameras at 11 different sites in Østmarka in Southern Norway. Insect visitation studies have traditionally relied on strenuous manual observations. The goal of this study was to evaluate the use of time-lapse cameras as an alternative to manual observations of beetle activity on polypores, something which has not previously been attempted.

Despite various technical difficulties and a high proportion of images being of poor quality (> 60%), the time-lapse cameras were able to generate a large amount of high-quality image data, from which the activity of three beetle species could be estimated. The image quality did not allow for detailed taxonomical identification of small beetle species (> 5 mm), so time-lapse cameras should be seen as a supplement to traditional methods as opposed to a complete replacement. The method can without doubt be improved and developed further. Time-lapse cameras thus have great potential for use in entomological research focusing on fungus-insect interactions.

Contents

1. Introduction

1.1 Fungus-insect interactions in dead wood

Fungi are the major contributors to dead wood decomposition in boreal forests (Floudas et al., 2012; Hoppe et al., 2016; Jacobs & Work, 2012). Wood-decay fungi not only colonise and decompose dead wood, but also transport and redistribute carbon and other nutrients underground. Insects, especially beetles, can play a direct role in dead wood decomposition, but their primary role is likely indirect, through fungus-insect interactions (Birkemoe et al., 2018). Beetles can facilitate the colonisation of dead wood by fungi by damaging and weakening living trees and can aid in the dispersal of fungi by transporting fungal propagules to newly dead wood (Castello et al., 1976; Harrington et al., 1981; Pettey & Shaw, 1986).

Dead wood is an essential component of a functioning forest ecosystem (Jonsson et al., 2012; Lassauce et al., 2011; Lonsdale et al., 2008). It is involved in processes such as nutrient recycling, carbon storage, and acts as a habitat for countless species of fungi, invertebrates, mosses, etc. (Bader et al., 1995; Thunes et al., 2000). Due to the large number of species connected to decaying wood, first and foremost a wide variety of fungi and insects (Eckelt et al., 2018; Lachat et al., 2012; Stokland et al., 2012), the volume of dead wood is widely used as an indicator of forest biodiversity (Junninen & Komonen, 2011; Lassauce et al., 2011; Siitonen et al., 2000). In the 2015 Norwegian Red List for Species, 2 355 species are classified as threatened, 47.6% of which are found in forests (Henriksen & Hilmo, 2015). As we are facing enormous challenges related to biodiversity loss and habitat degradation (Brondizio et al., 2019; Meyer et al., 2015), the understanding of the function and dynamics of dead wood systems, including the ecologically important interactions between fungi and insects, is of great importance going forwards.

Compared to the field of plant-insect interactions, a topic on which we have extensive knowledge, fungus-insect interactions are largely uncharted territory (Schigel, 2012). Outside a few well-known mutualistic interactions, the specificity of fungus-insect interactions has generally been assumed to be low (Hackman & Meinander, 1979; Hanski, 1989; Lacy, 1984). However, insects living inside fruiting bodies of polypores constitute a notable exception (Birkemoe et al., 2018; Fossil & Andersen, 1998; Kaila et al., 1994; Komonen, 2001; Lawrence, 1973; Orledge & Reynolds, 2005; Paviour-Smith, 1960; Yamashita et al., 2015). Studies on the host use of fungivorous insects show that beetles that feed on bracket fungi are usually monophagous or oligophagous (Jonsell & Nordlander, 2004; Orledge & Reynolds, 2005;

Paviour-Smith, 1960). Thorn et al. (2015) found that ciid beetles were closely associated with host fungi, with a level of specialisation comparable to parasites or phytophages and their hosts. In a study by Jacobsen et al. (2018a), saproxylic beetles, i.e. beetles that depend on dead wood, were sampled from recently cut aspen logs, and fungal DNA was extracted from each individual beetle. They found that the degree of specialisation exhibited between the insects and wood-decay fungi identified was similar to earlier estimates for animal-mediated seed dispersal networks. Smaller observational studies have revealed that beetles visiting common polypore species to feed also exhibit host preferences (Hågvar, 1999; Johansson et al., 2006).

Beetles visit living polypore fruiting bodies for a variety of reasons, including feeding and breeding purposes (Hågvar, 1999; Komonen et al., 2004; Schigel, 2011). Breeding species usually live in dead sporocarps, although some species may breed in dead or weakened parts (Jonsell et al., 2001; Økland & Hågvar, 1994). Only a few species are known to breed in living sporocarps, such as the staphylinid beetle *Gyrophaena boleti* (L.), whose larvae live in the pores on the underside of sporocarps of *Fomitopsis pinicola* (Sw.) P.Karst (Hågvar, 1999; Hågvar, 2018). Many beetles visit polypores during sporulation to feed on spores or to predate on other animals (Hågvar, 1999; Schigel, 2011). In most cases, the beetle visitors breed in dead wood, and not the sporocarp itself (Hågvar & Økland, 1997; Hågvar, 1999; Kaila, 1993). Kaila (1993) proposed that polypore-associated beetles may follow the sporocarp's odour to find their breeding substrate (a kairomone effect).

Spores of saproxylic polypore fungi are assumed to be primarily wind dispersed (Norros et al., 2012; Norros et al., 2014; Nuss, 1982; Seibold et al., 2019; Stenlid & Gustafsson, 2001). However, it is possible that wood-living beetles that visit polypores for opportunistic feeding of spores can act as vectors for fungal dispersal (Halbwachs & Bässler, 2015; Hågvar & Økland, 1997; Hågvar, 1999; Jacobsen et al., 2017; Talbot, 1952). *F. pinicola* releases larger amounts of volatiles during sporulation than during inactive phases (Fäldt et al., 1999). If insects are important for spore dispersal, this increase in volatiles could be adaptive for the fungus by attracting insect vectors. By utilizing beetles whose habitat preferences are similar to those of the fungus as dispersal vectors, the spores may have a higher likelihood of reaching a favourable spot where they can germinate (Seibold et al., 2019). Spores or mycelial fragments can get stuck to the exoskeleton and be transported by the beetle to a suitable substrate in another location (Castello et al., 1976; Harrington et al., 1981; Jacobsen et al., 2017; Pettey & Shaw, 1986). Furthermore, spores of certain species are able to retain viability through the insect's digestive tract and can thus be transported internally (Schmid et al., 2019; Talbot, 1952; Tuno, 1999).

Several authors argue that the importance of this mode of dispersal might be underestimated (Hågvar & Økland, 1997; Jacobsen et al., 2017; Lilleskov & Bruns, 2005; Talbot, 1952).

Although many questions remain unanswered, it is apparent that beetles have an ecologically important effect on fungal communities. In a study by Jacobsen et al. (2018b), exclusion of invertebrates from dead wood over two years significantly affected the fungal community composition in the logs. This suggests that beetles and other invertebrates may be important for the colonisation of saproxylic fungi. Despite the apparent importance of beetle visitors for fungal activity, we know little of who these visitors are, when and how often they visit, how long a typical visit lasts, etc.

1.2 Camera trapping as a monitoring method

Data collection of species interactions has traditionally been conducted on-site by human observers (Steen, 2017). This imposes several limitations on both the quality and the amount of data that can be collected. First and foremost, manual observations are time-consuming and require the human observer to be physically present on the study site. This makes it difficult to achieve a sufficient sampling effort, and monitoring over large spatiotemporal scales is usually impossible (Pegoraro et al., 2020).

For insect visitation studies, insects must either be identified *in situ* or be physically collected for later identification. This requires effort on the part of the observer, who must also find time to write notes in real time, taking their focus off the focal interactions or animals in question (Pegoraro et al., 2020; Steen, 2017). This is complicated further when insect visits happen frequently and simultaneously. When large amounts of data are recorded this way, the loss of some data is unavoidable. Additionally, the presence of a human observer may itself affect the behaviour of the focal animal (Iredale et al., 2010; Osztreiher, 1995; Pereira et al., 2016). These problems can be circumvented by monitoring insects remotely, e.g. by using cameras. Automatically triggered cameras can produce great volumes of data on animals in their habitats, but often at the cost of poor image quality (Gomez et al., 2016).

The use of cameras to monitor wildlife activity is nothing new. The first camera trap was invented already in the 1890s (Shiras, 1906). Their use for conservation and scientific purposes quickly caught on (Chapman, 1927; Dodge & Snyder, 1960) and today, cameras are widely used in ecological research that focuses on larger, vertebrate animals (Huang et al., 2014; Meek et al., 2014; O'Connell et al., 2010; Rovero et al., 2013; Steen & Barmoen, 2017). Since the first appearance of commercial wildlife cameras in the early 1990s (Kucera & Barrett, 1993),

rapid advancements have been made in the way behavioural studies of mammals and birds are conducted. Today, the widespread availability of affordable video monitoring equipment enables large amounts of long-term image and video data to be amassed continuously and non-invasively across multiple sites (Jones & Raphael, 1993; Rowcliffe & Carbone, 2008; Steen et al., 2011). However, using wildlife cameras to monitor insects is still a relatively new method in ecological research (Pegoraro et al., 2020).

Most conventional camera traps use a passive infrared sensor for their trigger, i.e. a sensor which measures infrared light emitted from objects that generate heat (e.g. a bird or a mammal), (Pegoraro et al., 2020). Although this can work reliably when monitoring big game, this technology is not viable for monitoring ectothermic or small endothermic animals (Hobbs & Brehme, 2017). Several methods have been devised to circumvent this (Azarcoya-Cabiedes et al., 2014; Steen et al., 2011). Many of these methods rely on video motion detection, i.e. continuous video that is automatically processed on site by a connected computer. Motion is detected by comparing frames of video for differences, and only when motion is detected will the footage be stored (Steen, 2017). The obvious drawback to this approach is the high consumption of electric energy that is required for running such equipment over time. In remote locations with limited access to on-grid electricity, battery capacity is a major limiting factor (Rovero et al., 2013). Another limitation is that small and slow-moving animals may be more easily overlooked, thus introducing a bias towards bigger and faster-moving animals. An alternative to these methods is use of time-lapse cameras, i.e. cameras that shoot images or video at regular intervals (Arjea et al., 2019; Suetsugu et al., 2017; Wiley & Kohler, 1981).

There are few studies on camera based monitoring of insects in the literature, and the majority of studies focus on plant-pollinator interactions (Høye et al., 2020b; Mann et al., 2019; Steen et al., 2011; Steen & Mundal, 2013; Steen, 2017; Suetsugu et al., 2017; Tran et al., 2018). In a recent study by Schmid et al. (2019), insect visits to seven mushroom species were surveyed using time-lapse cameras. Several studies focus primarily on methodological challenges and their solutions (Høye et al., 2020a; Høye et al., 2020b; Steen, 2017).

1.3 Study questions

In this project, I will test the possibility of using time-lapse cameras to monitor beetle activity on fruiting bodies of *Fomitopsis pinicola* in spruce forests in south-eastern Norway.

By using this method, I aim to answer the following questions:

I. Will time-lapse cameras be able to take photos of sufficient quality to estimate beetle activity on the hymenium of living fruiting bodies of *Fomitopsis pinicola*?
II. Is it possible to identify beetles to species from the images?

In addition, given that I am able to collect enough high-quality images, I will try to answer the following questions:

III. Can we infer ecological and behavioural information about individual beetle species from the image data, e.g. temperature preferences, the duration of visits, etc.?
IV. Does the recorded beetle activity reflect the quality of the surrounding habitat?

2. Materials and methods

2.1 The study species

To study beetle activity on polypore fruiting bodies (sporocarps), I used a common polypore brown-rot fungus on Norway spruce (*Picea abies* (L.) H.Karst.) *Fomitopsis pinicola* (Sw.) P.Karst. (Ryvarden & Melo, 2017). In addition to being common, *F. pinicola* is easy to detect, so suitable sites for monitoring were easily found. The density of *F. pinicola* fruiting bodies is higher in old-growth forest than in managed forests (Blaser et al., 2013; Komonen et al., 2004). Bacause *F. pinicola* is both common and conspicuous, it is a commonly chosen study species for entomological research (Hågvar & Økland, 1997; Hågvar, 1999; Jonsell & Nordlander, 1995; Komonen, 2003; Krasutskii, 2007; Thunes et al., 2000).

Sporocarps of *F. pinicola* are long-lived perennials. Individual sporocarps may live to an age of at least 18 years (Hågvar, 2008). Therefore, they represent relatively stable habitats for beetles and other insects that may live or feed on the hymenium layer. The sporulation period of *F. pinicola* starts in early spring, when temperatures exceed 0°C, and can last until the mean temperature drops below 0°C again in the autumn (Nuss, 1986). The rate of sporulation is at its highest in early spring and decreases once the mean temperature reaches its highest point, remaining at a low level for the rest of the sporulation period (Nuss, 1986). Small peaks can occur in autumn in certain years (Hågvar, 1999).

2.2 The study area

The study was conducted in Østmarka in south-eastern Norway from May 14th to September 22nd, 2019. To capture variation in the quality of the surrounding habitat, e.g. with regards to volume of dead wood, four areas were chosen, two within nature reserves (Ramstadslottet and

Østmarka) and another two (Skurvåsen and Morterud Lake) outside the reserves (Fig. 2.1). Within each area, I chose three sites based on the following criteria: 1) The site should consist of spruce-dominated old-growth forest with at least two sporocarps within a radius of 10 meters and, 2) sites should be separated by at least 100 meters. Three sites were chosen for camera placement within each of the four areas. Only two sites were found in Skurvåsen that satisfied the requirements. Thus, I ended up with a total of 11 sites (Fig. 2.1). For each site, the volume of dead wood and the number of sporocarps of *F. pinicola* in the surrounding area were recorded by another student (Reenskaug, 2020).

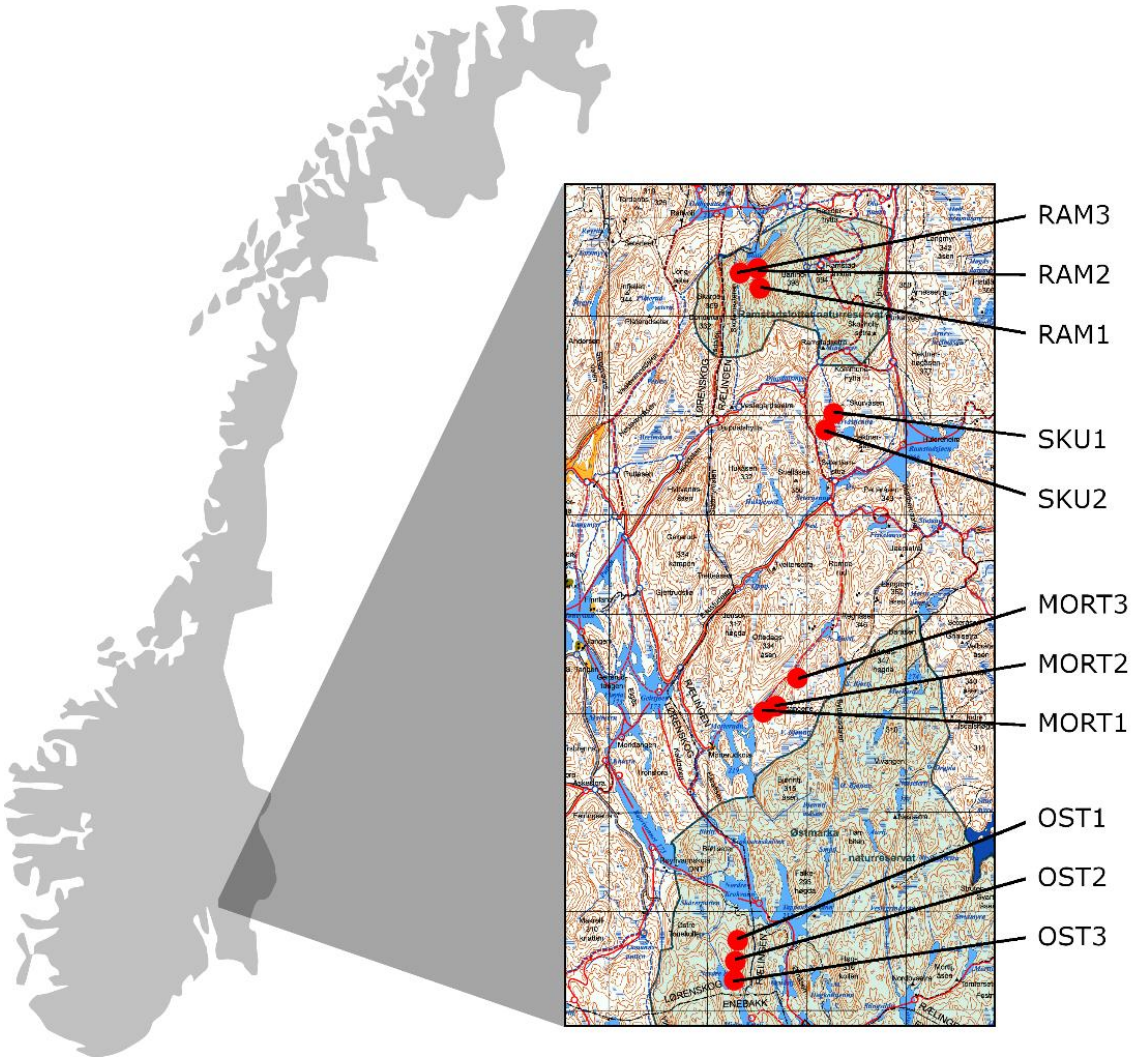


Figure 2.1. The 11 sites chosen for monitoring beetle activity on *Fomitopsis pinicola* sporocarps. The areas in green are Ramstadslottet (RAM) and Østmarka (OST) nature reserves. Skurvåsen (SKU) and Morterud Lake (MORT) lie outside of the nature reserves.

2.3 Experimental design

At each of the eleven sites, three fruiting bodies of *F. pinicola* were chosen. These were *1)* the "camera sporocarp", *2)* the "control sporocarp" and *3)* the "sticky-trap sporocarp". The control sporocarp was included in the study to account for the potential effect of the camera's presence on beetle behaviour, e.g. beetles being scared away by the flash. The sticky trap sporocarp was included to compare the use of time-lapse cameras to a more traditional trapping method. All sporocarps were growing on spruce snags. Due to a lack of suitably sized sporocarps in the area, the sticky trap sporocarp was omitted from the site SKU2.

A time-lapse camera of the type Wingscapes® TimelapseCam Pro Digital Camera (Moultrie WCT-00126) was mounted on the trunk beneath each camera sporocarp on a camera mount custom made for this investigation by the Technical department at the Norwegian University of Life Sciences (NMBU) (Fig. 2.). The camera model has a built-in white LED flash function that activates automatically under low light conditions. In order to capture roughly the same surface area of the hymenium with each picture, each camera was mounted with ca. 20 cm between the lens and the hymenium. Due to the smaller size of some of the sporocarps chosen, the hymenium layer did not fill the entire frame in every site. Because of this, the surface area captured differs slightly between camera sites. All cameras were set to take pictures regularly at ten-minute intervals throughout the day. Temperature was recorded at the time of capturing for each individual picture using the camera's internal thermometer. The cameras were active from May 14th to June 19th, and from July 31st to September 22nd, though the exact activation date for some cameras vary by a few days.

Between May 23rd, 2019 and June 19th, 2019, I made manual visits to all 11 study sites at various times of the day, and all beetle visits to control sporocarps were registered. At least one visit was made to each site during the night, i.e. between 21:00 and 06:00. Each site was visited on average 6.5 times, but only 2.3 times on average at night.

Sticky traps were mounted on the top and bottom of the "sticky-trap sporocarp" in each location. Each sticky trap consisted of a 2 cm by 5 cm clear plastic strip that was covered in glue (Tree Tanglefoot® Insect Barrier). These were mounted between May 14th and May 23rd and collected on June 19th.

Figure 2.2. The camera setup used in this project. A time-lapse camera is mounted to a spruce trunk at an angle, taking a picture of the sporulating surface every ten minutes. The photo was taken at a test site that was not in the final project. Photo: Tone Birkemoe

2.4 Terminology and a few clarifications

I define an observation as one individual sighting of a beetle in one single image. According to this definition, two beetles captured in one image count as two observations, while ten successive images of the same beetle would yield ten observations. I also use the less specific term "activity" when discussing my findings. A challenge faced when relying on a time-lapse image series is deciding how a visit is defined. When beetles are collected in the field, a visit can be easily defined, i.e. each collected beetle represents one visit, with no risk of recording the same beetle twice. In this study, because photos are taken at such frequent intervals and beetles are not physically removed, we are likely to observe the same individuals across several consecutive images. This introduces the potential to observe a beetle's behaviour, but also introduces a risk of pseudoreplication when attempting to quantify beetle visits. For this reason, I differentiate between the term "visit" and the terms "observation" and "activity" as defined above. The term "visit" is reserved for times when visits are discussed directly, e.g. when estimated the number and duration of visits.

2.5 Identifying 'good' images.

Due to various challenges to the image quality, e.g. sun glare, condensation and rain, a large portion of the images were not convenient for my intended purposes. I was either not able to identify arthropods to order level, or not able to detect them at all. However, the distinction between images of 'good' and 'bad' quality is not clear. Determining whether an image is 'good' or 'bad' is conditional and depends on blurriness, light intensity, direction of sunlight how much of the image is blurry, and several other factors (Fig. 2.3).

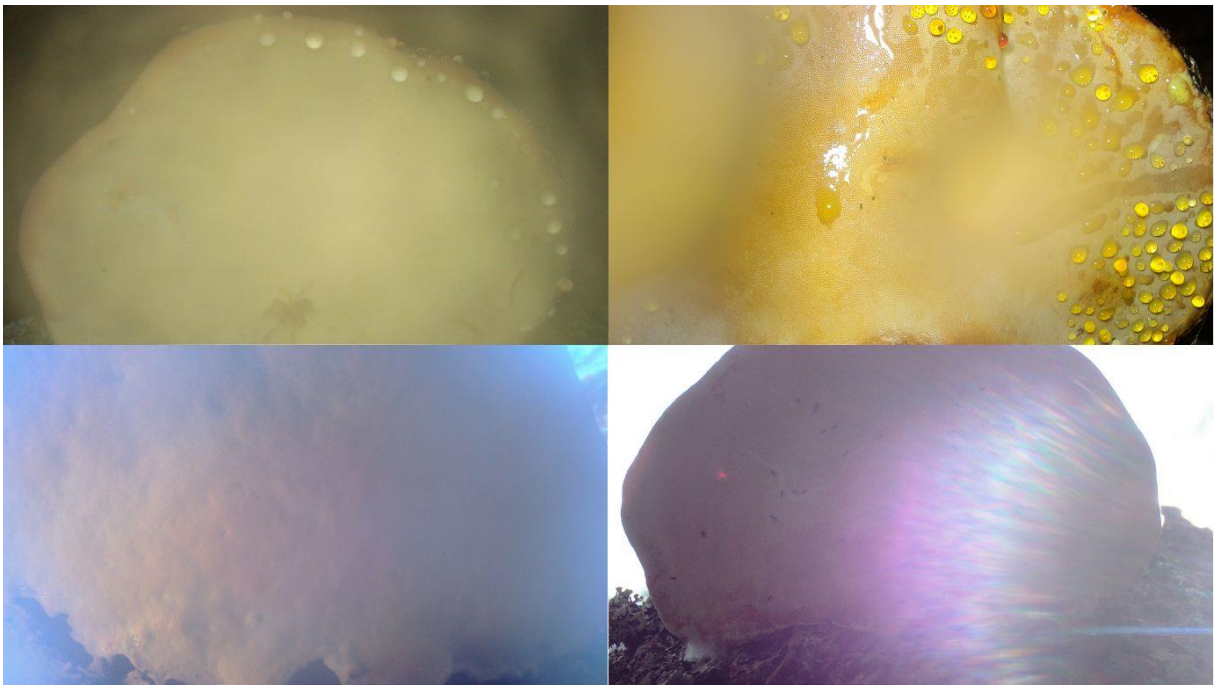


Figure 2.3. Examples of images that can be difficult to categorise as either good or bad.

Manually sorting photos according to image quality requires a huge manual effort. Therefore, I used a Python script that calculates the Variance of Laplacian (VL) of each image and sorts them into separate folders depending on their VL value (Appendix A). VL is used to detect image blur, and depends on an edge detection algorithm to give an estimate of an image's sharpness, which can be used as an estimator of image quality (Bansal et al., 2016; Pech-Pacheco et al., 2000). Without a point of reference, the VL value alone cannot determine the quality of an image. Therefore, a VL threshold value had to be defined. Images with a VL value below the threshold were automatically discarded, leaving only the 'good' images for manual inspection.

To define a reasonable VL threshold value, the script first had to be taught what a 'good' image looks like. A subset consisting of 123 images were manually chosen to represent 'good' images. I aimed to capture as much variation as possible in what a 'good' image could look like (e.g. time of day, light conditions, individual differences between sporocarps, colour, condensation, etc.). The VL threshold value was calculated from these images based on the following formula:

$$Mean\ VL - Standard\ deviation\ of\ VL$$

This calculation resulted in a provisional VL threshold value of ~ 4.156. To measure how accurately the script was able to categorise images with this threshold value, I compared its performance with that of three human observers on a subset consisting of 2 000 randomly

drawn images from the full data set. The three observers grouped the images subjectively into either the "good" or "bad" category. Since the purpose of this exercise was to create a script that could replace human efforts and thereby save time, I hoped to find the VL threshold value that would result in a performance close to that of a human observer. I compared the categorisations of the human observers and the script with the Pearson correlation coefficient (Table 1.1.).

Table 1.1. A subset of 2 000 images were sorted into two categories of image quality by three observers and a fitted script (Appendix A). The association between observers and the script was calculated using the Pearson correlation coefficient.

	Observer 1	Observer 2	Observer 3	Script
Observer 1	1.0000000			
Observer 2	0.7770894	1.0000000		
Observer 3	0.7037062	0.7499435	1.0000000	
Script	0.5127791	0.4944605	0.5104457	1.0000000

The three human observers were more correlated with each other than with the script, which was far more lenient than the human observers. The script categorised as many as 959 images as good, compared to the average of 739 images between all three human observers. Although the script did not perform well when using the provisional VL value, I did not have time to improve it further.

2.6 Preparation of data

All images classified as good by the VL-based script were annotated using the VGG Image Annotator (VIA) tool (Dutta & Zisserman, 2019). The VIA software allows human annotators to define and describe spatial regions in images. In practice, this means that an annotator goes through every image individually and outlines regions that can then be assigned a class (e.g. species identity) (Fig. 2.4.). Non-focal invertebrates were identified to group (i.e. "snail", "spider", etc.). Beetles were identified to species whenever possible and were later validated by an expert. Annotations can be exported to a plain text data file in either JSON or CSV format, which can then be imported into other software (e.g. R) for further processing.

Figure 2.4. A screenshot of the VGG Image Annotator tool in action, which is used to manually annotate images. The image contains a *Thymalus limbatus* (upper left) and a cluster of *Gyrophaena boleti* (upper right). An outline has been manually drawn around the beetle and its species identity defined as *T. limbatus*. The same was done for every focal observation in every good image.

2.7 Statistical analysis

All diagrams and statistical analyses were produced in the R programming environment, version 3.5.3 (R Core Team, 2017). I chose to only analyse observations data from *Thymalus limbatus* since I obtained the most observations of that species (*See 3.2. Beetle visitors to the polypores*). The observation data of *T. limbatus* was analysed using a Generalised Linear Mixed Model (GLMM), using the 'glmer.nb' function in lme4 package version 1.1-21 (Bates et al., 2014). My response variable consists of count data (i.e. frequency of observations of *T. limbatus* per site per 10 min.) and is assumed to follow a Poisson distribution. Therefore, I chose to use a Generalised Linear Model (GLM), since it handles non-normal error distributions (Zuur et al., 2009). For a normal Poisson distribution, the variance is equal to the mean. This is often not the case with biological data. For data sets or models where the variance exceeds the mean, the term overdispersion is used (Ver Hoef & Boveng, 2007). To deal with overdispersion in my count data, I used a quasi-Poisson model (Zeileis et al., 2008). I chose to use a Mixed Model since it allows me to interpret predictor variables as either fixed or random

effects (Henderson Jr, 1982). My study design is nested, i.e. camera sites are situated within study areas. I expect more variation between than within areas, e.g. MORT1 is expected to be less similar to RAM1 than to MORT2. I account for that variation by including camera site as a random effect. Flash / no flash was not included as a variable in the model since it was found to be highly correlated with time of day. The two Skurvåsen sites (SKU1 & SKU2) were excluded from this analysis because *A)* the sites in Skurvåsen did not conform to the criteria for study site quality (see *2.2 Study Area*) and *B)* because no observations were made from the two sites.

My aim with the analysis was to answer Study Question II (See *1.3 Study questions*). I used model selection to identify which variables best explain the variation in my response variable. I created eight candidate models, and chose the *best model* based on the Bayesian Information Criterion (BIC), i.e. the one with lowest BIC value. The model favoured by BIC essentially corresponds to the model which is rendered most plausible by the data at hand (Neath & Cavanaugh, 2012). I used the Akaike information criterion (AIC) to validate the BIC (Akaike, 1973). After finding the *best model*, I used the squared standardised regression coefficients to quantify the relative contribution of each predictor variable in the model (Afifi et al., 2003).

The time of day was recorded as a continuous linear variable of each minute of the day (1 – 1440). If 'Minute of day' were fitted as a predictor in the GLMM, the response would increase/decrease linearly with the minute of day, meaning that the greatest difference in the response would be between 'Minute of day' = 1 and 'Minute of day' = 1440. Instead, I created the predictor variable 'Daily oscillation' to represent cyclic time (Fig. 2.5.). 'Daily oscillation' was represented by two oscillatory transformations of 'Minute of the day'. The transformations were done by using single frequency cosine (cos 1) and sine (sin 1) functions[1] (Fernandez et al., 2014).

Nine covariates were tried with the model selection, including fixed effects, statistical interactions, and 'Site ID' as the random effect (Appendix B; Table B.1.). The fixed effects were 'Day of year' (DOY), 'Temperature', 'Volume of dead wood', 'No. of sporocarps', 'Study area' and 'Daily oscillation'. 'Daily oscillation' was tested for interactions with 'Temperature'. 'DOY', 'Daily oscillation', and 'Temperature' were included as fixed variables, and 'Site ID' as a random variable in *all* candidate models.

[1] 'Daily oscillation' (sin 1 ∨ cos 1) = (2 × π × sin ∨ cos × 'Minute of day' × x) / 1440, where x = the frequency of the function (in this case 1).

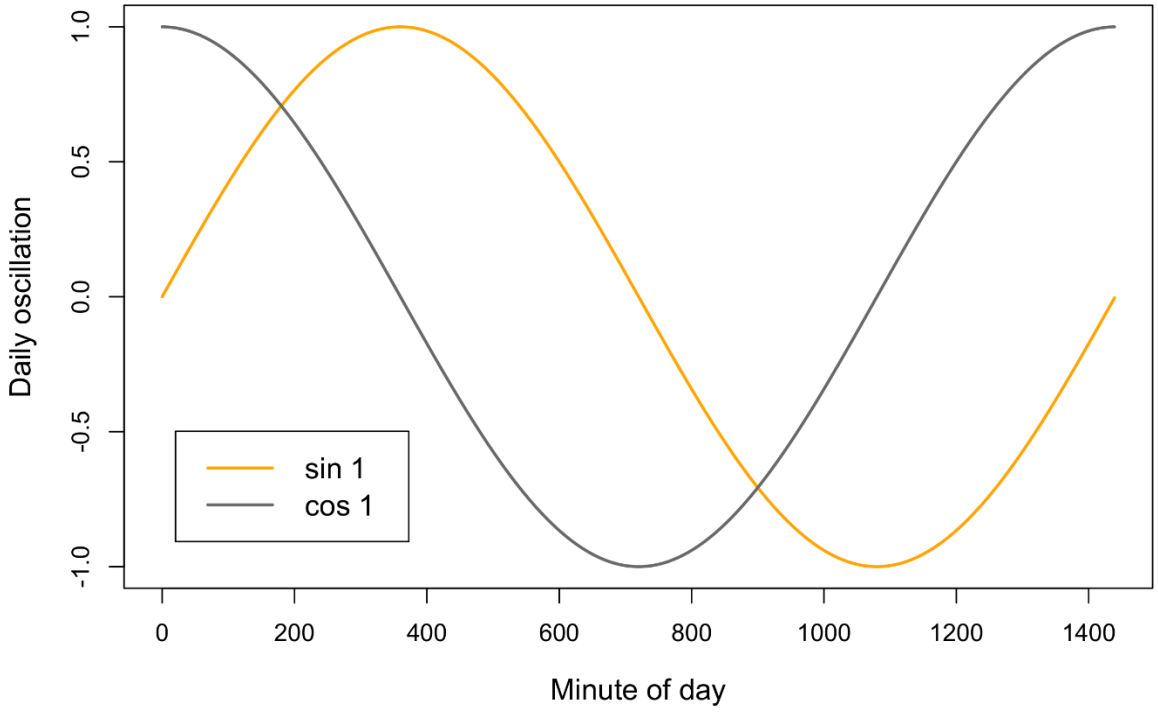


Figure 2.5. Visualisation of the predictor variable 'Daily oscillation'. Daily oscillation (cos 1) peaks at midnight. Daily oscillation (sin 1) is identical to Daily oscillation (cos 1) but is offset by ¼ cycle.

2.8 Estimating the number and duration of visits for common species

To estimate the number of visits for a species, I defined a visit as a number of consecutive images with the same individual beetle remaining in the frame. For this to work, I make the following assumptions:

1) When a beetle is observed across two consecutive images, I assume that they are the same individual and that the individual was also present in-between images.

2) If the number of individuals increases, I assume that all individuals from the previous image are still there.

Since I am not tracking individual beetles across images, I do not know which individual leaves if the number of individuals decreases, i.e. I do not know which visit ends. To keep it simple, whenever the number of individuals decreases by at least one from the previous image, I treat all visits from that image as having ended, and any number of observations from the present image as new visits. Because visits are occasionally "split" this way, the number of visits is likely to be overestimated while the mean duration of a visit is likely to be underestimated. Since images are taken at ten-minute intervals, ten minutes is the smallest possible increment

of time. To estimate the duration of a visit in minutes, the number of consecutive images is simply multiplied by ten.

3. Results

3.1 Image quality – selecting images for further analyses

From May 14th to June 22nd, 2019, the time-lapse cameras took 84 354 images across all sites (Fig. 3.1.) I encountered various problems when using the time-lapse cameras, including water intake (OST2, August) and cameras that turned themselves off early during the experiment (RAM3 and OST1, May/June). Several cameras also had drastically lower battery capacity than advertised. Because of these problems, I ended up with far fewer images than expected. The camera located at OST1 was replaced after the first period of the field season and a setup error unfortunately left the data from this camera invalid.

Image quality varied greatly between camera sites, with the percentage of good images ranging from 6.0% to 57.3% (Table 3.1., Fig 3.2.). There were only three sites where more than half of the images were good. Image quality also varied within-site depending on external factors such as time of day (Fig. 3.3.). In general, and from all but one site, a higher percentage of images taken during the night were classified as good than of those taken during the day (Table 3.1., Fig 3.3.).

Approximately half of the images fell beneath the Variance of Laplacian (VL) threshold and were automatically discarded, leaving 41 157 images for manual annotation. During the annotation process, around 20% of these were identified as false positives and discarded. After annotation was completed, data from 30 290 good images was left to be analysed further, i.e. 35.9% of the total number of images.

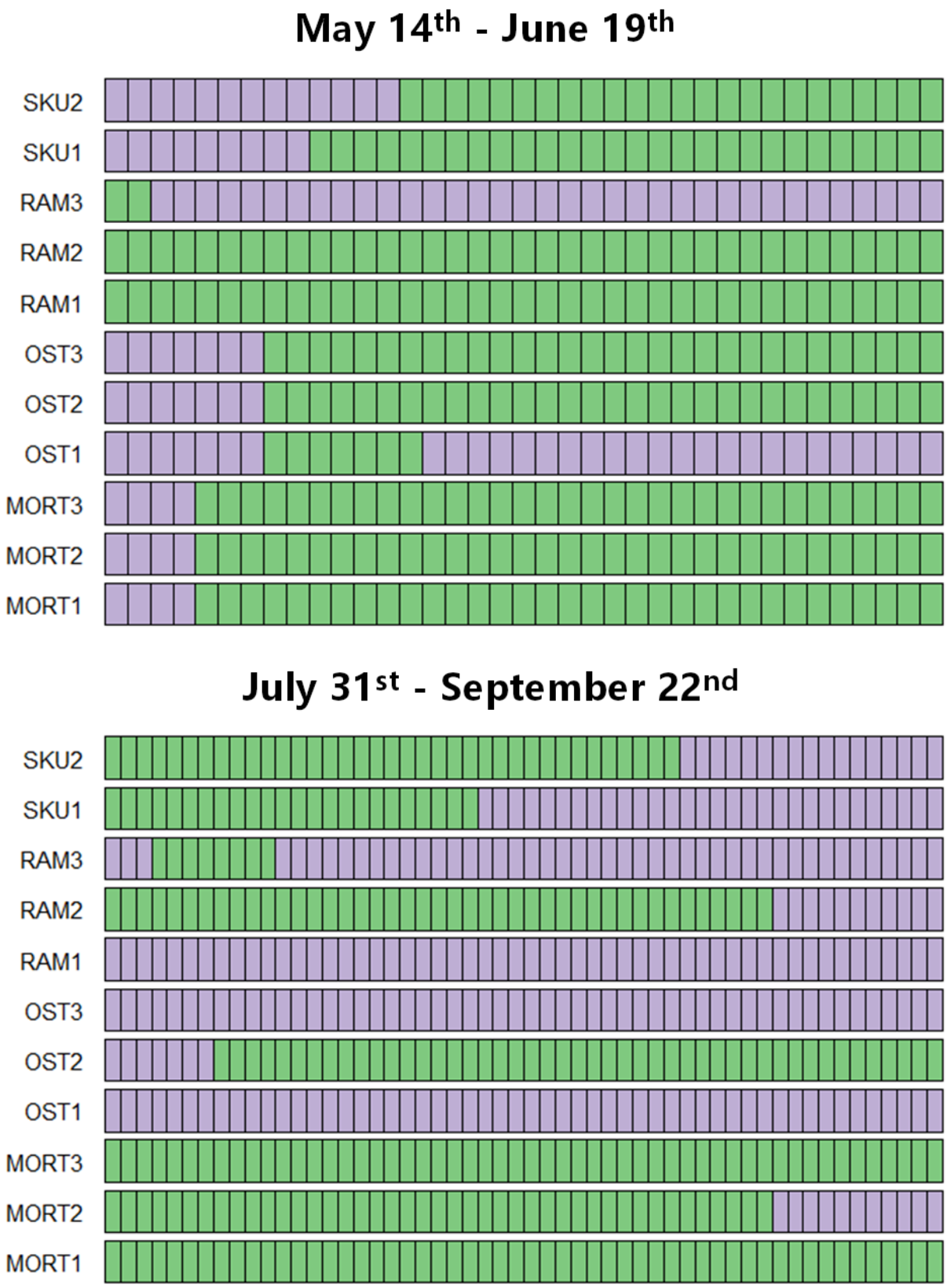


Figure 3.1. Overview of when the cameras were working from each of the 11 sites, between May 14th – June 19th (top) and July 31st – September 22nd (bottom). Each cell represents 24 hours; a green cell signifies that at least one photo was taken on that day.

Table 3.1. Number and percentage of good images taken during day and night for each site (total number of images in parentheses). Day = 06:00 a.m. – 08:59 p.m., Night = 09:00 p.m. – 05:59 a.m.

Site ID		No. of good images		% good images	
		Day	Night	Day	Night
MORT1	(12 241)	1 263	1 640	16.5%	35.7%
MORT2	(10 677)	2 666	1 271	39.9%	31.8%
MORT3	(12 246)	4 122	2 893	53.8%	63.0%
OST1	(911)	58	204	9.9%	62.8%
OST2	(10 772)	1 907	1 661	28.3%	41.2%
OST3	(4 198)	360	216	13.7%	13.8%
RAM1	(5 179)	1 197	855	37.0%	44.0%
RAM2	(11 268)	2 242	2 452	31.8%	58.2%
RAM3	(1 065)	195	374	29.6%	92.4%
SKU1	(7 266)	2 070	2 126	45.4%	78.7%
SKU2	(8 529)	289	227	5.4%	7.1%
ALL SITES	**(84 354)**	**16 369**	**13 919**	**31.0%**	**44.1%**

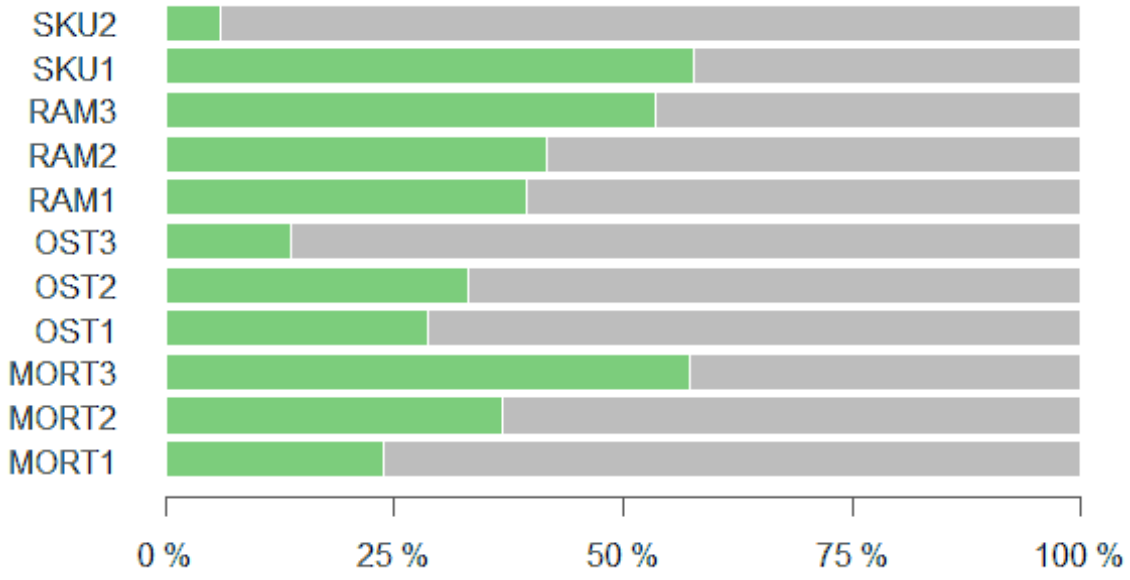


Figure 3.2. Overview of the distribution of good / bad images for each of the 11 sites. The green portion of each bar represents the percentage of images from the respective site that were "good", i.e. deemed to be good enough for it to be possible to identify arthropods from the image.

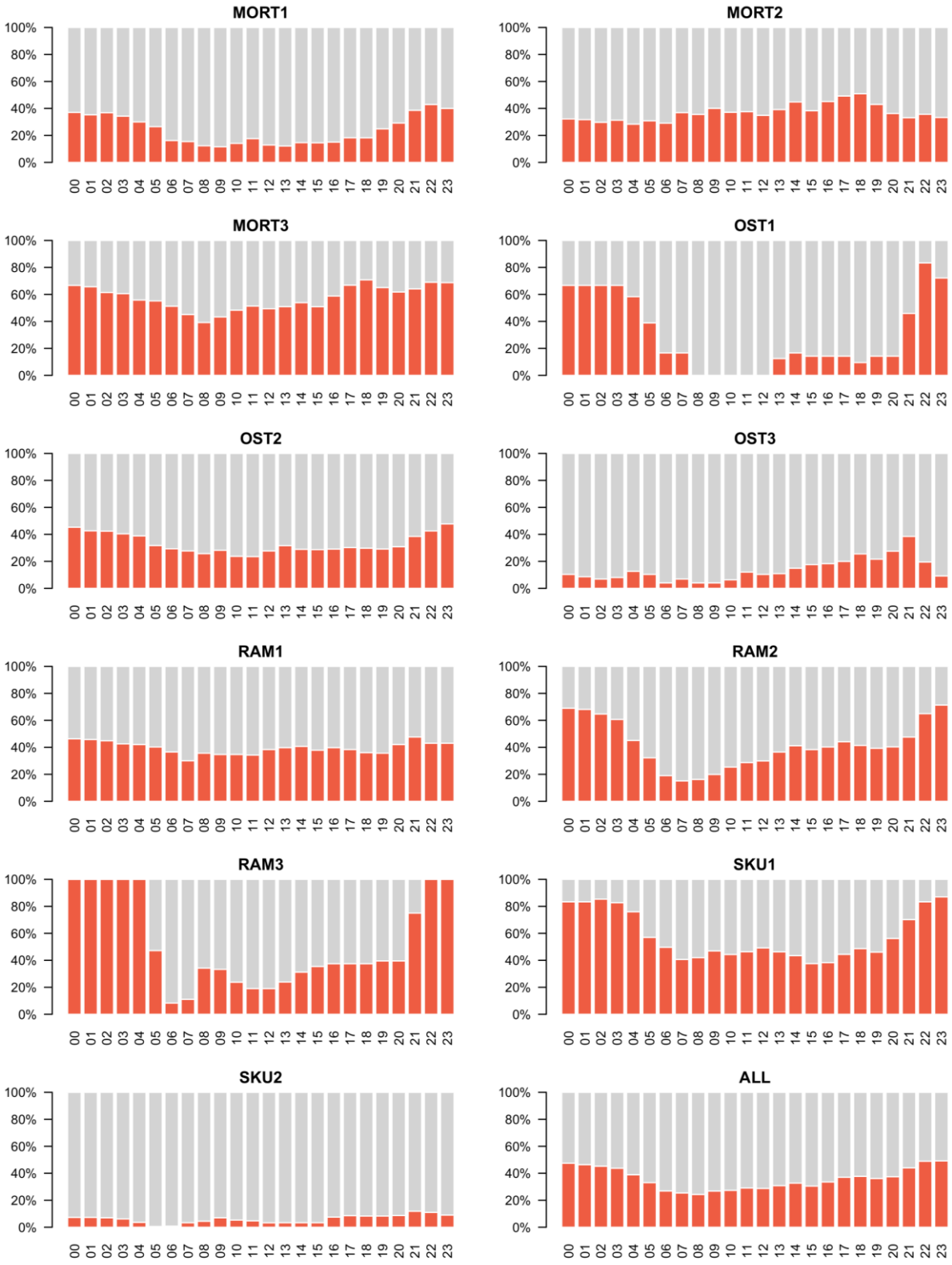
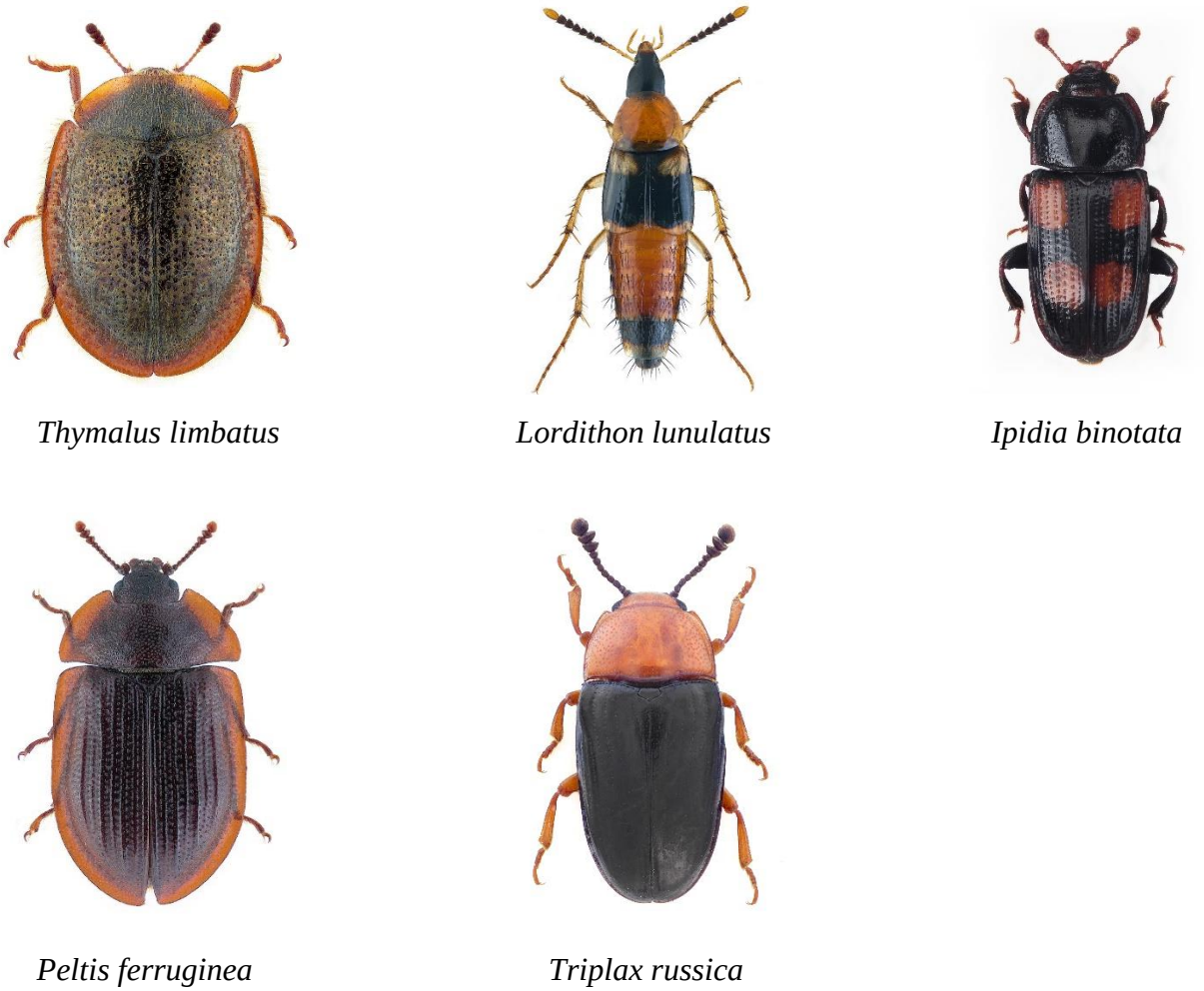


Figure 3.3. Distribution of good images throughout the day for each camera site. The x-axis represents hour of the day (24h), beginning at midnight. The y-axis represents percentage of good images (in red) taken at each respective hour. The panel in the lowermost right shows the combined numbers across all sites.

3.2 Beetle visitors to the polypores

I identified beetles from 1 373 (4.54%) of the good images and made a total of 1 650 individual observations (Table 3.2.). I was able to identify five species which were validated by an expert: *Thymalus limbatus*, *Lordithon lunulatus*, *Ipidia binotata*, *Peltis ferruginea* and *Triplax russica* (Fig. 3.4, Table 3.2.). The number and frequency of observations varied greatly between sites, both in total and for individual species (Table 3.3.). No observations were made in Skurvåsen (SKU1 & SKU2).



Thymalus limbatus *Lordithon lunulatus* *Ipidia binotata*

Peltis ferruginea *Triplax russica*

Figure 3.4. The species that were identified from the time-lapse images, *Thymalus limbatus*, *Lordithon lunulatus*, *Ipidia binotata*, *Peltis ferruginea* and *Triplax russica*. Images are not to scale. The images are licenced under Creative Commons: *T. limbatus*, *L. lunulatus* and *P. ferruginea* by Dr. Udo Schmidt licensed under CC BY-SA 2.0, *I. binotata* by Stanislav Snäll licensed under CC BY 3.0. *T. russica* by John Hallmén licensed under CC BY 3.0.

Table 3.2. Overview of all beetle species identified from the time-lapse images, the number of observations for each species, and whether they were observed during night or day. "Unidentified species" includes all species that were not identified to the species level.

Family and species	No. of observations	Presence Day/Night
STAPHYLINIDAE		
Lordithon lunulatus (L.)	219	DN
NITIDULIDAE		
Ipidia binotata Reitter	90	DN
EROTYLIDAE		
Triplax russica (L.)	2	D
TROGOSSITIDAE		
Peltis ferruginea (L.)	1	N
Thymalus limbatus (Fabricius)	1 130	DN
Unidentified species	208	
SUM ALL BEETLES	1 650	

Table 3.3. Number of observations per 100 images for each site, of *Thymalus limbatus*, *Lordithon lunulatus* and *Ipidia binotata*, and the total number of beetles (incl. unidentified species). Number of observations are in parentheses. No observations were made in Skurvåsen (SKU1 & SKU2).

Study site	*T. limbatus*		*L. lunulatus*		*I. binotata*		**Total**	
MORT1	26.46	(768)	0.14	(4)	–		27.73	(805)
MORT2	–		–		–		0.38	(15)
MORT3	1.43	(100)	–		0.16	(11)	1.77	(124)
Sum MORT	**6.26**	**(868)**	**0.03**	**(4)**	**0.08**	**(11)**	**6.81**	**(944)**
OST1	–		–		–		–	
OST2	4.57	(163)	0.25	(9)	1.68	(60)	7.20	(257)
OST3	–		0.52	(3)	3.30	(19)	3.82	(22)
Sum OST	**3.70**	**(163)**	**0.27**	**(12)**	**1.79**	**(79)**	**6.33**	**(279)**
RAM1	1.32	(27)	9.84	(202)	–		11.74	(241)
RAM2	1.34	(63)	0.02	(1)	–		3.62	(170)
RAM3	1.58	(9)	–		–		2.81	(16)
Sum RAM	**1.35**	**(99)**	**2.78**	**(203)**	**–**		**5.84**	**(427)**
SKU1	–		–		–		–	
SKU2	–		–		–		–	
Sum SKU	–		–		–		–	

The highest number of visits was recorded for *T. limbatus*, of which an estimated 260 visits were recorded (Table 3.4.). The duration of visits varied greatly between the three species. The longest visits were recorded for *T. limbatus*. In contrast, more than 50% of *L. lunulatus* visits consisted of single-image observations, with the longest recorded visit consisting of only six consecutive images.

Table 3.4. The estimated number of visits, the 1st quartile, median and 3rd quartile of estimated visit duration (i.e. number of consecutive images), and the longest estimated visit duration for each of the three most observed species in the study.

Species	No. of visits	Quartiles of duration of visits			Longest visit
		1st	Median	3rd	
Thymalus limbatus	260	1	2	5	95
Lordithon lunulatus	118	1	1	2	6
Ipidia binotata	19	1	3	4.5	19

3.3 Manual observations and sticky traps

No beetles were caught in any of the 10 sticky traps mounted on the hymenium of the "sticky trap sporocarps" between May and June 22nd (the traps did however catch a decent number of spruce needles, the leg of a crane fly and a couple of mosquitoes). I observed six beetles on the hymenium during my manual observations of the "control sporocarps" (Table 3.5.). Four of these were identified to species.

Table 3.5. All individuals observed during control trips made between May 23rd, 2019 and June 19th, 2019. Four individuals were identified to species.

Date	**Time**	**Site ID**	**Species**
26.05.2019	02:15 p.m.	MORT1	–
31.05.2019	02:39 p.m.	RAM3	*Peltis ferruginea*
16.06.2019	03:27 a.m.	RAM2	*Peltis ferruginea*
16.06.2019	03:47 a.m.	RAM2	*Peltis ferruginea*
16.06.2019	03:47 a.m.	RAM3	–
19.06.2019	01:16 p.m.	SKU2	*Thymalus limbatus*

3.4 What determines the activity level of Thymalus limbatus, Lordithon lunulatus and Ipidia binotata?

The three beetle species *T. limbatus*, *L. lunulatus* and *I. binotata* all exhibit temperature preferences, although the pattern can be best seen with *T. limbatus* (Fig. 3.5.A.). Both *T. limbatus* and *I. binotata* were more frequently observed at night (Fig. 3.5.B.). It is apparent that I missed an important period of beetle activity when the cameras were shut down between June 19th and July 31st (Fig. 3.5.C.).

The best model to explain variation in *T. limbatus* activity on *F. pinicola* was favoured by both BIC and AIC (Table 3.6.). None of the site-specific explanatory variables, i.e. 'Study area', 'Volume of dead wood' and 'No. of sporocarps', were included in the best model. The 'Day of year', 'Daily oscillation', and 'Temperature' all had a significant positive effect on *T. limbatus* activity on *F. pinicola* sporocarps between May 14th and September 22nd, 2019 (Table 3.7.). There was also a significant effect of the statistical interaction between 'Daily oscillation' and 'Temperature'. 'Daily oscillation' and the statistical interaction between 'Daily oscillation' and 'Temperature' had the strongest effect, contributing to > 75% of the variation in *T. limbatus* activity (Table 3.8.).

Estimating from this model, the highest frequency of observations is expected at 1:11 a.m. (Fig. 3.6.). The expected frequency of observations nearly doubles when the temperature increases by ~ 3°C, from 0.3 to 0.6 expected observations per site per ten minutes. Few or no observations are expected outside the night hours regardless of temperature.

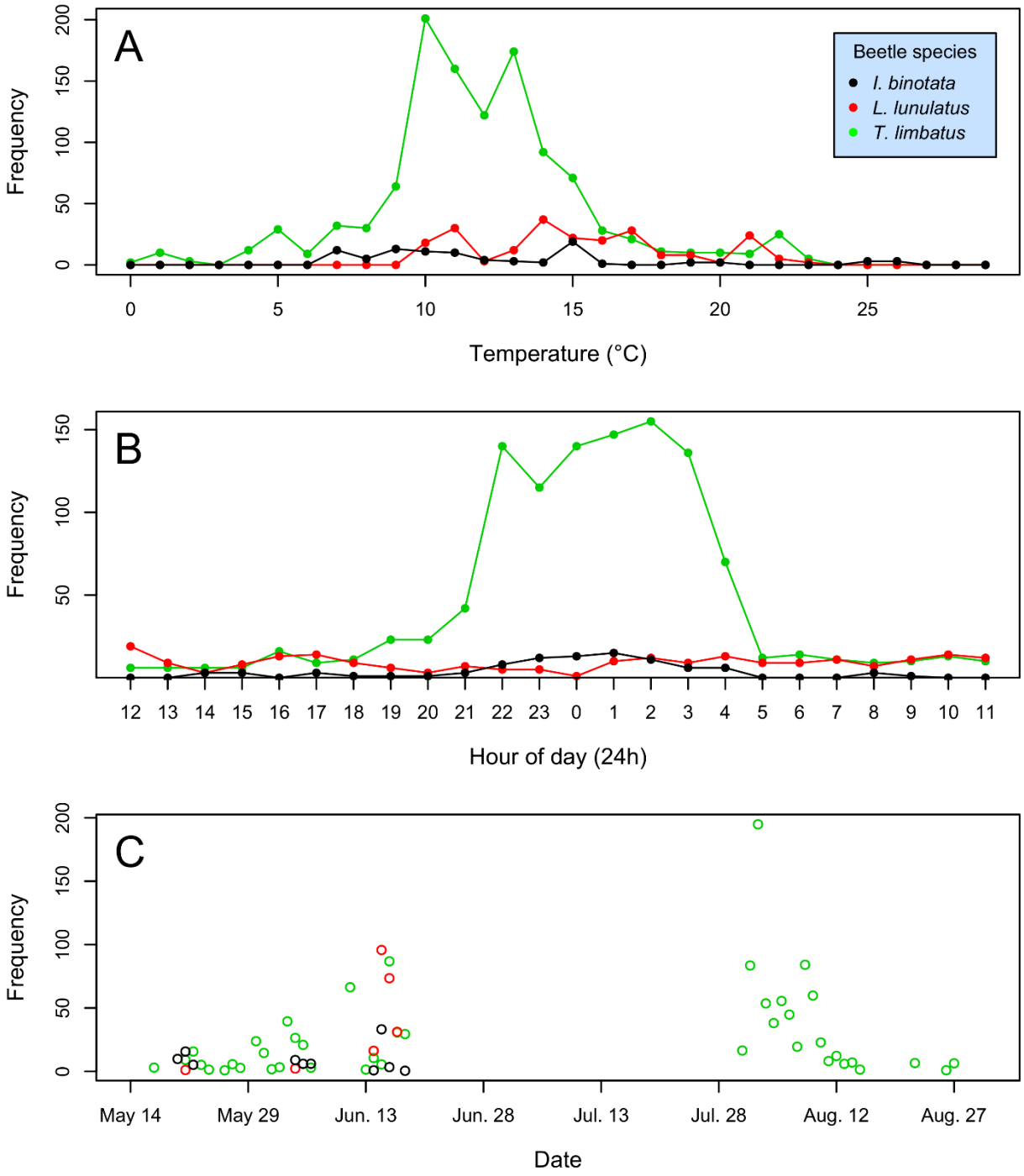


Figure 3.5. Observations of three beetle species, *Ipidia binotata*, *Lordithon lunulatus* and *Thymalus* limbatus, made using time-lapse cameras. **A)** Number of observations made at different temperatures ranging from 0°C to 29°C. **B)** Number of observations per hour throughout the day (24 hours). The x-axis has been centred around midnight. **C)** Number of observations per day between May 14th and August 31st. No observations were made of either species in September, so all dates from September 1st are excluded. Images were taken between May 14th and June 19th, and between July 31st and September 22nd, 2019.

Table 3.6. *A priori* generalised linear mixed effects models for observations of the trogossitid beetle *Thymalus limbatus* to sporocarps of *Fomitopsis pinicola*. X = term included in candidate model. BIC = Bayesian Information Criterion. AIC = Akaike Information Criterion. ΔAIC / ΔBIC = difference in BIC and AIC values respectively between the candidate model and the most parsimonious candidate model according to the respective criterion. Day of year, Minute of day and Temperature were included as fixed effects in all models. Site ID was always included as a random effect.

Day of year	Daily oscillation	Temperature (°C)	Study area	Volume of dead wood	No. of sporocarps	Daily oscillation × Temperature	**BIC**	**ΔBIC**	**AIC**	**ΔAIC**
X	X	X	X	X	X	X	6376.0	30.2	6278.2	5.8
X	X	X	X	X		X	6375.2	29.4	6277.4	5.0
X	X	X		X	X	X	6365.9	20.1	6276.2	3.8
X	X	X			X	X	6355.9	10.1	6274.4	2.0
X	X	X	X			X	6365.1	19.3	6275.4	3.0
X	X	X		X		X	6355.7	9.9	6274.3	1.9
X	**X**	**X**				**X**	**6345.8**	**0**	**6272.4**	**0**
X	X	X					6411.3	65.5	6354.2	81.8

Table 3.7. Generalised Linear Mixed Model output[a] of *Thymalus limbatus* activity on sporocarps of *Fomitopsis pinicola* from May 14th to September 22nd, 2019 [b].

Fixed Effects	Estimate	Std. Error	z score	p-value
Intercept	-9.5167314	0.9737343	-9.773	< 0.001
Day of year[c]	0.0108164	0.0009604	11.262	< 0.001
Temperature	0.2143675	0.0139746	15.340	< 0.001
Daily oscillation (sin 1)	1.1897799	0.2072642	5.740	< 0.001
Daily oscillation (cos 1)	3.7176921	0.2492297	14.917	< 0.001
Temperature × sin 1	-0.0050317	0.0148718	-0.338	0.735
Temperature × cos 1	-0.1478838	0.0154565	-9.568	< 0.001

[a] No. of observations ~ Day of year + (Temperature × Daily oscillation [sin 1 + cos 1]) + (1|Site ID).

[b] The best model according to a BIC model selection procedure (Table 3.6.).

[c] Day of year is fitted as a continuous predictor.

Table 3.8. Variance contribution (%) of covariates in a generalized linear mixed model of *Thymalus limbatus* activity on sporocarps of *Fomitopsis pinicola* from May 14th to September 22nd, 2019.

Covariate	**Variance contribution**
Daily oscillation[a]	58.5%
Site ID	19.2%
Daily oscillation × Temperature	14.7%
Temperature	6.2%
Day of year	1.4%

[a] The summed variance contribution of both daily oscillation variables (cos 1 + sin 1). See *2.7 Statistical analyses*.

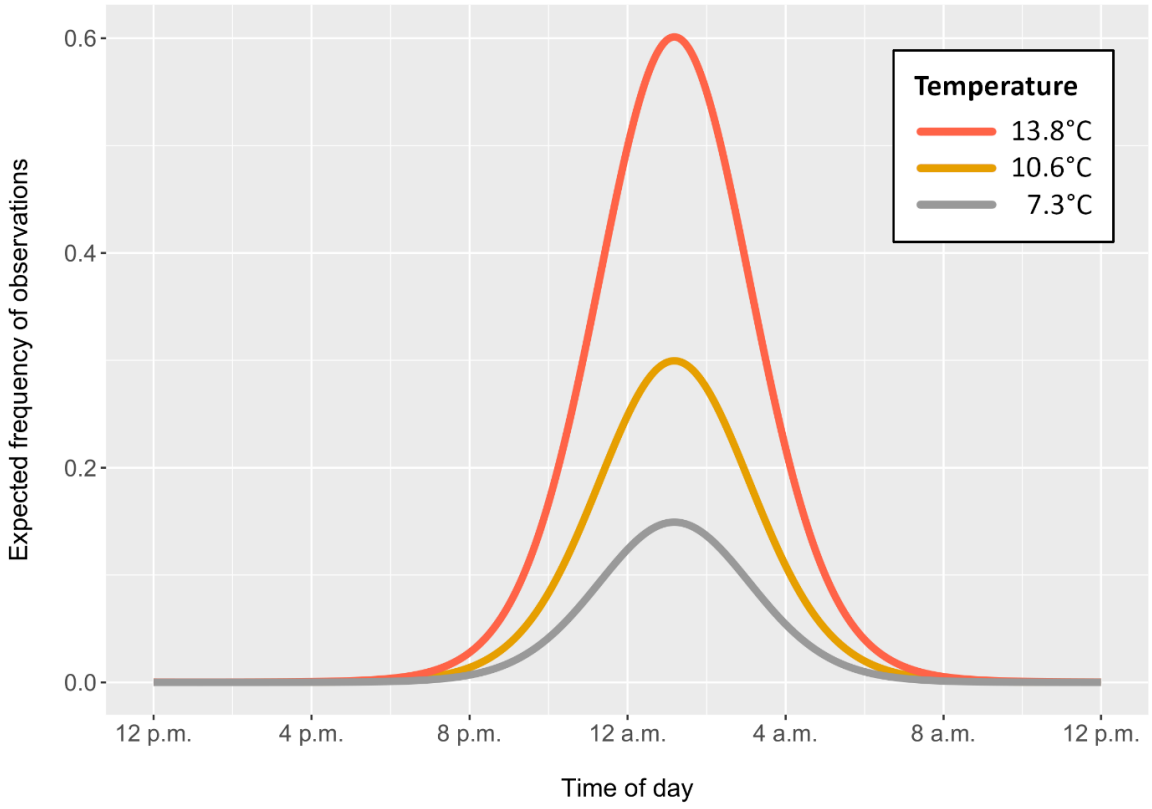


Figure 3.6. Expected frequency of observations per camera per 10 min. on August 8th, 2019 of *Thymalus limbatus*, throughout the day and at three different temperatures. The temperatures represented by line colour are the mean night-time (between 9 p.m. and 6 a.m.) temperature for the study period (orange line, 10.6°C), and the mean night-time temperature ± the standard deviation in night-time temperature (red line, 13.8°C and grey line 7.3°C, respectively.).

4. Discussion

4.1 Camera performance and automated categorisation of image quality

In this study, I used time-lapse cameras to monitor beetle activity on sporulating fruiting bodies of *Fomitopsis pinicola*. In total, 84 354 images were collected. Of these, 35.9% (30 290 images) were good enough to identify arthropods. Five large and characteristic beetle species could be easily identified to species level from the images (*Thymalus limbatus*, *Lordithon lunulatus*, *Ipidia binotata*, *Peltis ferruginea* and *Triplax russica*). Smaller species proved more difficult to identify. Condensation, sun glare and overexposure due to strong flash were among the chief reasons for discarding images (Appendix C). The problems I faced with sun glare were likely exacerbated by the unorthodox placement of the cameras. Several previous studies have experimented with a horizontal placement of camera traps (Høye et al., 2020a; Nichols et al., 2017; Smith & Coulson, 2012; Taylor et al., 2014), but with the lens facing the ground, unlike the present study. Neither of these sources report difficulties with condensation or sun glare.

The time-lapse cameras performed better at night (Table 3.1., Fig. 3.3.). Hågvar (1999) found that beetle activity on *F. pinicola* is highest around midnight. High performance is therefore most essential during the night-time hours.

During the project, I encountered various technical issues with the time-lapse cameras. Several cameras had drastically lower battery capacity than advertised. Others turned themselves off early due to unknown causes. These issues collectively hurt data collection by directly reducing the amount of data that could be generated, and by effectively reducing the number of replicates (i.e. camera sites) in the study (Fig. 3.1.). Newey et al. (2015) experienced similar issues with obstruction of the lens due to condensation and rain, and even experienced rapid depletion of the battery in cold weather and camera failure due to unknown causes. Although camera traps and similar technology is widely used in ecological research, it is seldom the focus of the study. The constraints and limitations of camera technology, including equipment failure, are rarely acknowledged in published papers (Meek et al., 2015). If the technical issues are grave enough and lead to data being of insufficient ecological value to the study, the study may not be published at all. This means that information about technical issues is unlikely to emerge in the scientific literature. Newey et al. (2015) concludes that many issues relating to the use of camera technology in research stem from the use of cheaper models instead of more expensive, professional equipment. The development of commercial wildlife cameras has largely been driven by the needs of hunters, and cheaper equipment rarely meets minimum standards for scientific application (Meek & Pittet, 2013).

Replicates are essential in ecological research, since ecological systems are inherently variable (Quinn & Keough, 2002). Because of this, multiple camera setups are often needed for conducting camera surveys. Cost per unit is one of the most influential factors driving the choice of camera model by researchers (Meek, 2012). In essence, researchers forfeit quality in favour of quantity when purchasing equipment, since this allows them to cover a greater number of sites.

As part of the camera setup for the present project, a plexiglass cover was mounted above the camera lens in order to protect it from water and dust (Fig. 2.2.). A rubber ring was set tightly between the plexiglass and the camera to prevent water from entering and obscuring the lens. Due to miscommunication with the technical department, the rings we got for the finished camera mounts were made of foam instead of rubber (which had been used in the prototype). These foam rings were not impervious to water, causing water droplets to be caught between the plexiglass cover and the lens. This resulted in poor image quality across all sites until the

problem was identified and fixed in early June. This mistake likely cost me a substantial number of ‘good’ images from May (Appendix E; Table E.1.).

One of my major goals during the project was the automatic detection and removal of blurry or otherwise unusable images, to reduce the amount of time spent on manual annotation. Early on, my supervisors and I considered training a neural network to perform this task, but this was ultimately deemed beyond the scope of my project. I ended up using a script based on the Variance of Laplacian (VL) to filter out blurry images. About 64% of the images were discarded from the ensuing analyses. Of these, about four fifths, or 41 157 images, were automatically discarded prior to annotation by the VL script. The remaining fifth, or 10 867 images, were false positives which were manually removed from the data set during annotation. This is problematic since the manual annotation of images is very time consuming. Additionally, when bad images need to be assessed and removed manually, we risk introducing observer bias. Although I do not have an estimate of their number, I suspect that some good images were falsely discarded as well.

One weakness in my method was the way the VL threshold value was chosen. The threshold value was calculated based on the mean VL of a subset of only 123 images specifically selected to cover as much of the variation as possible in what could be considered a “good” image. This subset was originally created to test the viability of the method and included images from all eleven sites. I believe that the accuracy would have improved significantly if I had used different VL threshold values for each camera site based on images from that respective site alone. There is much variation between sites in the quality and composition of their images, e.g. in colour variation of both the hymenium and the backdrop, ratio of hymenium to sky in an image, exposure of a camera to sunlight, etc. This means that there is also a certain variation in what a “good” image will look like depending on the site from which the image originates. Assessing the quality of an image can be very difficult, even with the experience of having looked through several hundreds and even thousands of them. Ironically, the most reliable indication that an image is bad is the presence of a blurry insect. When attempting to improve the subset of images from which the VL threshold value was calculated, I placed emphasis on including good, yet difficult images. This emphasis worked against its intent. By including difficult images in the subset, the mean VL was pushed towards the limit between good and bad images, leading to the inclusion of a greater number of “edge cases” which could realistically have tipped either way. For future studies, I would recommend setting the VL threshold value higher, leading to a more conservative inclusion of images. Considering the

large amount of data that can be collected when time-lapse cameras are used, the loss of some images is not critical. Even after more than 60% of the images were discarded, I had more individual observations than I could feasibly have made in the same amount of time, had I relied on manual observations alone. However, it might not be possible to detect all focal visits if too many difficult images are included. This can lead to an artificial increase in the relative frequency of "no observation" results. The number of observations of large, characteristic species relative to that of smaller and cryptic species may similarly become inflated due to the higher difficulty in detecting and identifying such specimens.

Although the main criterion I set for including an image was that it should be possible to identify an arthropod from the image, several of the resulting images *did* contain beetles that were not possible to identify to species (Appendix D; Fig. D.4, Fig. D.5). These unknown beetles were mostly small (< 3 mm), making them hard to identify, even when a larger beetle could be clearly identified from the very same image (Fig. 4.1.). Schmid et al. (2019) had similar problems with identifying small beetle visitors to mushrooms from time-lapse images, attributing this to the combination of small animal size and low image resolution.

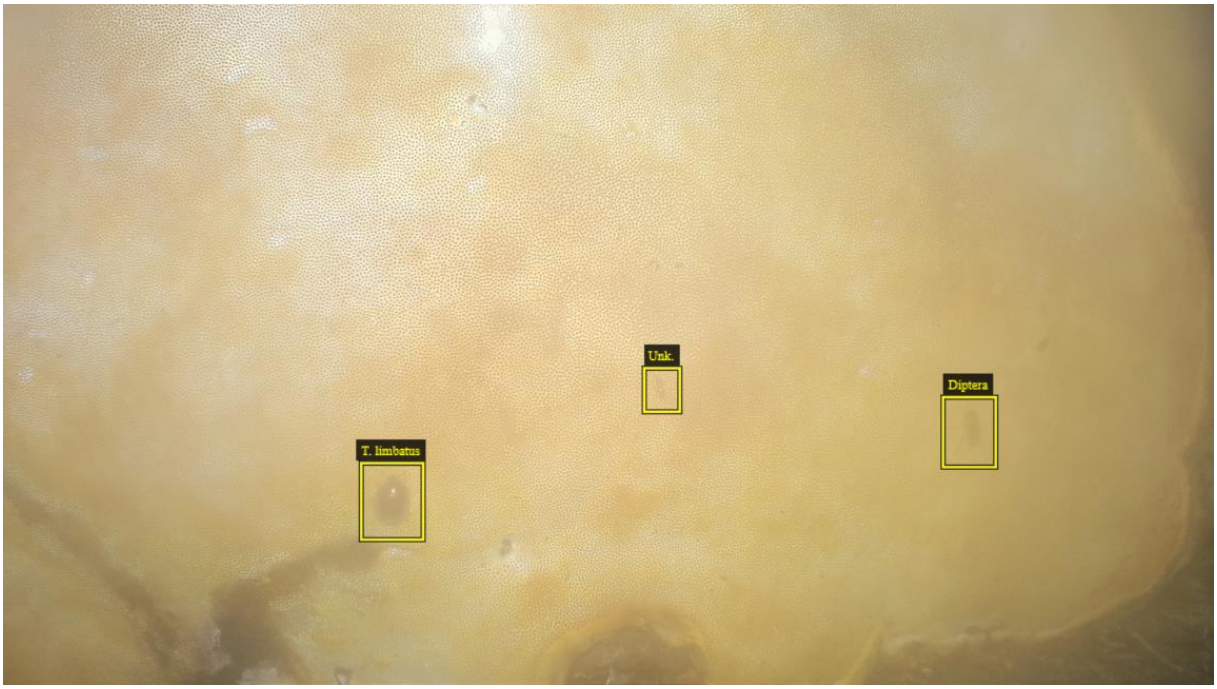


Figure 4.1. A *Thymalus limbatus* could be identified from this image (lower left), but it was not possible to identify the smaller beetle (*Unk.* for "unknown") in the middle of the image. Screenshot from the VGG Image Annotation tool.

4.2 Camera observations vs human observations

The study sites were distributed between four areas in order to capture variation in habitat quality. The differences between sites were pronounced, both in the number of recorded observations and which species were observed (Table 3.3.). This suggests that the species assemblage and relative abundance of species vary greatly between sites. This is further supported by the differences between my own findings and the findings from a previous study from Hågvar (1999), which was conducted in the same geographical area as the present study. Despite a large number of images, I only identified five beetle species. In comparison, Hågvar (1999) collected 27 unique beetle species from living sporocarps of *F. pinicola*. Several of the species found by Hågvar are very small and would likely have been indistinguishable from each other in the time-lapse image. For example, I was not able to identify Ciidae from my image data. The association between *F. pinicola* and ciid beetles, in particular *Cis glabratus* Mellié and *Cis quadridens* Mellié, has been well documented (Hågvar, 1999; Jonsell & Nordlander, 1995; Komonen et al., 2004; Lawrence, 1973). However, two species identified from my images were not found by Hågvar. These were the sap beetle *I. binotata* and the rove beetle *L. lunulatus*, which were recorded on *F. pinicola* several times in the present study (Table 3.2.).

I only made one observation of *P. ferruginea* from the images captured by the time-lapse cameras. I had expected to make many more observations of this species, as several previous studies have highlighted the association between *F. pinicola* and *P. ferruginea* (Hågvar & Økland, 1997; Hågvar, 1999; Krasutskii, 2007; Thunes et al., 2000). It is a possibility that visitation rates of *P. ferruginea* were negatively influenced by the presence of the time-lapse camera beneath the camera sporocarps. When disturbed, *P. ferruginea* individuals are prone to let go of the substrate and drop to the ground (Lunde, L.F., personal communication, July 2020) or hide (Hågvar, 1999). The automatic flash function could potentially be disturbing. Despite a relatively low number of manual visits (75), I collected three individuals of *P. ferruginea* from two control sporocarps during control visits to my study sites. I also observed several individuals of *P. ferruginea* on non-focal *F. pinicola* sporocarps during my stay in Østmarka. If the time-lapse camera influenced the presence of *P. ferruginea*, presence of other species may have been equally affected. This should be considered when evaluating further use of time-lapse cameras for insect monitoring at night.

It should be noted that despite the large sample size in the present study, the number of replicates is low. Despite my greater number of individual observations, Hågvar was able to monitor more sites, a total of 100 *F. pinicola* sporocarps in contrast to my 11 camera

sporocarps. The low number of replicates also made me more vulnerable to equipment failure. In the second period of camera activity, three cameras failed immediately (OST1, OST3 and RAM1). Additionally, the camera from RAM3 failed after only eight days of activity. The camera from SKU2, while technically working, produced virtually no good images in this period. These events essentially reduced the number of replicates for this period to just seven sites (Appendix E; Table E.2.).

The wildlife cameras as we used them are restricted in that they can only observe the underside of the sporocarp. While beetles collected from the polypore fungus *Fomes fomentarius* (L. ex Fr.) Kickx. are frequently found on top of the fruiting body, Hågvar (1999) found that almost all beetles sitting on living sporocarps of *F. pinicola* sat on the underside, i.e. on the hymenium. However, from my images I have observed that individuals of *T. limbatus* frequently sit along the edge of the sporocarps.

Remote cameras typically generate large amounts of bycatch data on non-focal species and interactions (Scotson et al., 2017). This data can be used to answer secondary research questions or be shared with collaborators for whom the data is relevant. Even when non-focal observations have not been transcribed from the image material, it can be extracted from the image material later, at little extra cost. Non-focal animals observed on the hymenium of *F. pinicola* in the present study include a variety of different species of spiders, harvestmen, centipedes, springtails, flies, slugs and *Gyrophaena boleti*.

4.3 Species ecology obtained from image analysis

According to Thunes et al. (2000), the amount of dead wood in the vicinity of a site is the major factor influencing beetle diversity in sporocarps of *F. pinicola*. I hypothesised that the level of beetle activity would correlate positively with volume of dead wood. I did not find an effect of either dead wood volume or number of *F. pinicola* sporocarps in the surrounding area on the number of observations of *T. limbatus*. This conforms with earlier findings that dead wood abundance is a poor predictor for saproxylic species richness and abundance at small spatial scales (Gibb et al., 2006; Schiegg, 2000; Siitonen, 1994; Økland et al., 1996). Reenskaug (2020) sampled beetles from the same sites and in the same timeframe as I, using window and malaise traps. She found that forest density was the most important factor influencing both beetle species richness and the total number of individuals collected. Neither volume of dead wood nor the number of sporocarps in the study site's vicinity affected the number of beetles caught.

Because different beetle species can differ greatly in their behavioural patterns, it can be somewhat problematic to directly compare the number of observations between beetle species. For example, individuals of *Thymalus limbatus* typically remain in one place for much longer than any of the other beetle species I recorded (Fig. 4.2.). Since beetles are not removed from the polypore with an observation, individuals are likely to be captured by several consecutive images. Without taking this into account, it would be easy to overestimate the actual activity level of *T. limbatus* relative to other species. I was able to estimate the number and duration of visits for *T. limbatus, L. lunulatus* and *I. binotata* by analysing the number of consecutive images with individuals in the frame (Table 3.4.).

However, estimates of visit duration are most likely slightly underestimated, and to different degree depending on species behaviour. For example, two or more *L. lunulatus* individuals were observed together relatively more often than *T. limbatus* individuals. Individuals of *L. lunulatus* also move more frantically around the hymenium in-between images (Fig. 4.3.), often repeatedly exiting and re-entering the frame. Because of the way visits were estimated, *L. lunulatus* visits were most likely 'split' much more often, and counted as shorter, more frequent visits. This issue was exacerbated by a flaw in the study design. Due to difficulties in finding similarly sized sporocarps, camera sporocarps varied considerably in size. To ensure that the area covered in the frame was comparable between cameras, each camera was mounted at roughly equal distance from the hymenium layer (ca. 20 cm). For large sporocarps, this meant that a considerable proportion of the hymenium was not in-frame. The camera sporocarp at the site RAM1 was one of the larger sporocarps in the study, and as much as 202 of the 219 observations of *L. lunulatus* derive from this site. It is very likely that when *L. lunulatus* individuals "left" the sporocarp, they were simply located elsewhere on the hymenium, and out-of-frame. For future studies, I would recommend mounting the cameras in such a manner that the majority of the hymenium is in-frame, regardless of sporocarp size. Differences in size can instead be addressed by treating size as a categorical predictor variable of beetle activity (e.g. small-medium-large).

There was frequent and heavy rainfall for most of the first period when the cameras were active, i.e. between May 14th and June 22nd. Aukema et al. (2005) found that exogenous weather factors strongly affected the flight activity of the pine engraver, *Ips pini* (Say), in the Great Lakes region of the United States. An excess of precipitation during flight periods of the hickory bark beetle, *Eccoptogaster quadrispinosus* (Say), resulted in a partial mortality of the adults

(George, 1929). The weather may have influenced my results by limiting beetle flight activity in the period when the cameras were active.

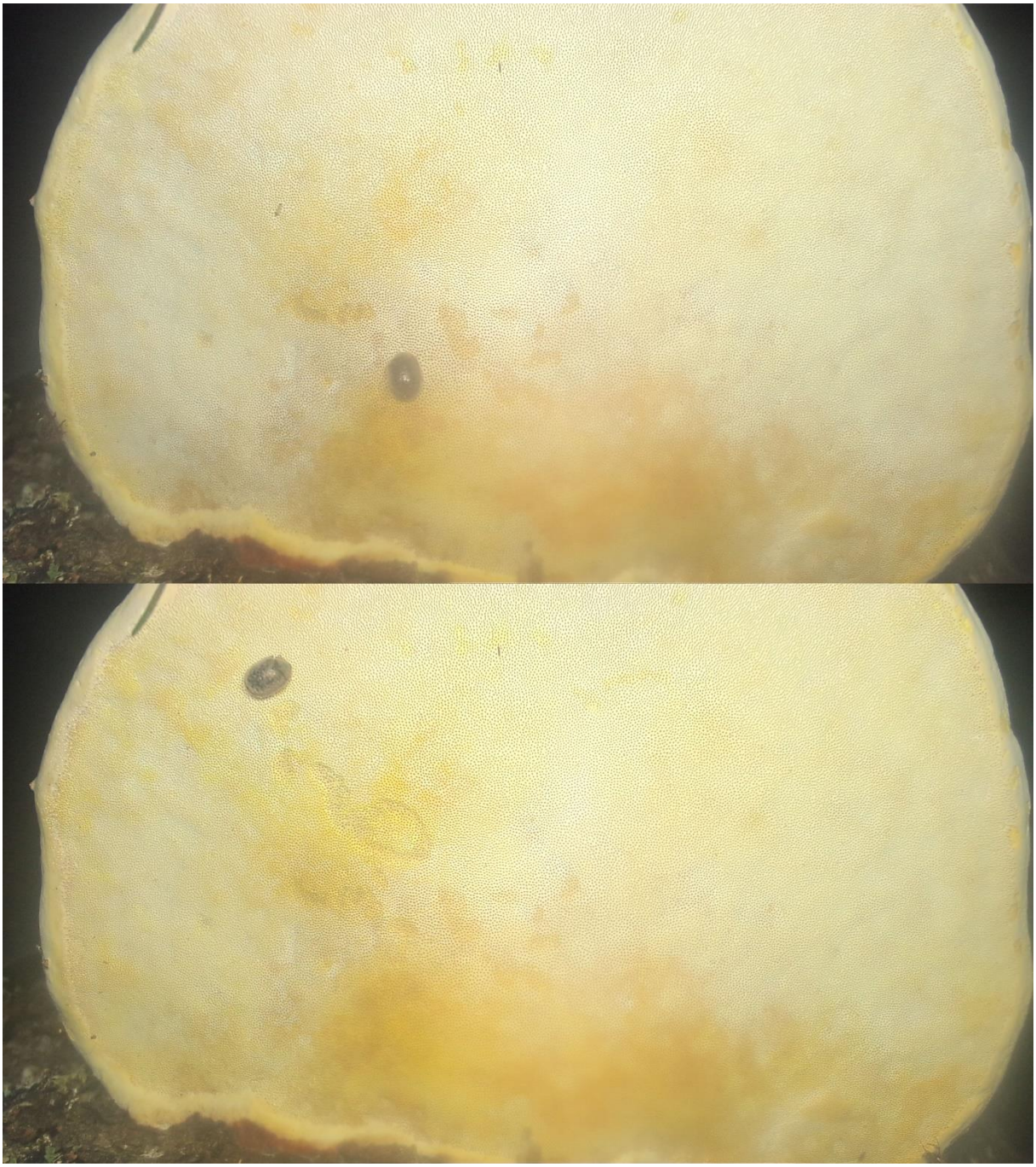


Figure 4.2. This *Thymalus limbatus* individual could be manually traced across 191 consecutive images. With images being taken at ten-minute intervals, that means it spent nearly 32 hours on the same sporocarp! It left a feeding trail that is clearly visible on the bottom image.

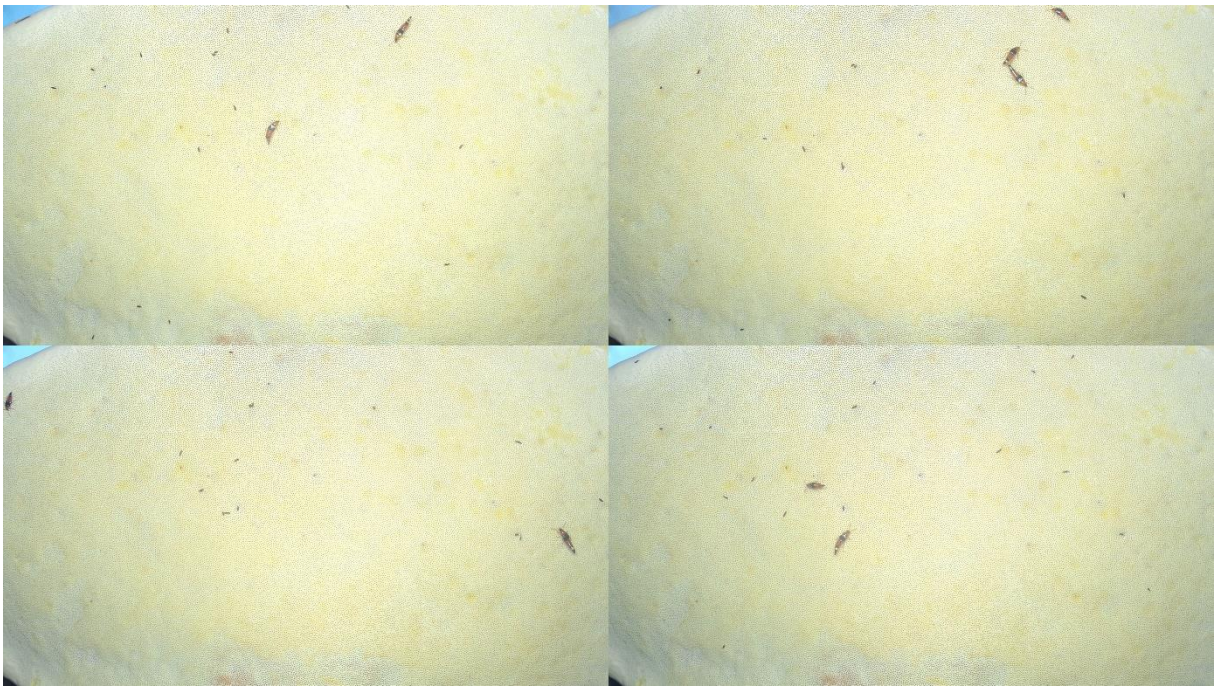


Figure 4.3. Four consecutive images of *Lordithon lunulatus* individuals visiting RAM1 (top to bottom and left to right). This species is predatory, and very active during visits. In comparison, spore-feeders typically appear more docile. Due to the large size of this camera sporocarp, much of the hymenium is out-of-frame.

In Germany, the sporulation period of *F. pinicola* lasts for approximately nine months, with the sporulation rate being at its highest prior to the beginning of June (Nuss, 1986). It is possible that the cameras should ideally have been active sooner in the spring in order to capture more of the temporal variation in beetle activity. Approximately a month before fieldwork started, different camera mount prototypes were tested in a forest in Ås, Norway. During these test runs, we observed many beetles. This may indicate that I missed an important period of beetle activity before my field season started. Additionally, I missed an important activity period between the first and second period when the time-lapse cameras were not active, i.e. between June 19th and July 31st (Fig. 3.5.C.). Gillespie et al. (2017) found that the flight activity of both *T. limbatus* and *I. binotata* peaked in late June.

Spore predation by beetles can have adverse effects on fungal reproductive fitness (Guevara et al., 2000). However, several authors have proposed a possible mutualistic relationship between certain fungi and spore-feeding beetles (Hågvar & Økland, 1997; Jacobsen et al., 2017; Seibold et al., 2019; Talbot, 1952). Calhim et al. (2018) concludes that the safe arrival of spores on specific substrates is a more important driver of evolution in spore morphology than the ability of spores to disperse far. This may suggest that the morphological traits that enable fungal

spores to be dispersed by insects are adaptive. Fungal dispersal by wind is stochastic and often limited in distance (Galante et al., 2011; Halbwachs & Bässler, 2015; Peay & Bruns, 2014; Talbot, 1952). Meanwhile, insect vectors are resource oriented (Hågvar, 1999; Jonsell & Nordlander, 1995). Komonen (2008) studied the abilities of ciid beetles to colonise *Trametes* in a lake-island system in eastern Finland. He found that ciids are able to disperse up to 1.5 km following the odours of their host fruiting bodies. In *F. pinicola* and *F. fomentarius*, the production of odorous metabolites increases during sporulation (Fäldt et al., 1999; Johansson et al., 2006). A similar increase in volatile production during sporulation has been detected in other fungal guilds as well (Börjesson et al., 1993).

I found that the time of day was the most important variable driving *T. limbatus* activity (Table 3.8.). The highest frequency of observations was expected at 1:11 a.m. (Fig. 3.6.). Additionally, both *T. limbatus* and *I. binotata* were most frequently observed at night. Hågvar (1999) documented increased activity at night in several beetle species visiting *F. pinicola* and *F. fomentarius*. Nocturnal activity in spore-feeding beetles might be correlated with the diurnal sporulation rhythm of their fungal hosts. Sporulation rhythms in fungi are often correlated with humidity, and therefore usually highest around midnight (Haard & Kramer, 1970; Halbwachs & Bässler, 2015; Oneto et al., 2020). Hågvar (1999) sometimes observed intense spore production around midnight in *F. fomentarius*. I did not observe a pattern of nocturnal activity in *L. lunulatus*. As adults, *L. lunulatus* are generalist predators on fungivorous beetles (Fäldt et al., 1999). They have been found to prefer *F. pinicola* sporocarps but are not attracted to volatiles emitted by mycelia of the same species (Johansson et al., 2006).

Several of the species that were identified from the time-lapse images are associated with old-growth forest and dead wood and are therefore potential spore dispersers. Both larvae and adults of *T limbatus* are known to feed on the mycelia of wood-decay fungi (Miłkowski et al., 2019). Adults are often found visiting sporocarps, where they feed on spores (Hågvar, 1999; Miłkowski et al., 2019). In the present study, *T. limbatus* could also be seen feeding directly on the hymenium of *F. pinicola* (Fig. 4.2.). Spores of *F. pinicola* can retain viability through the digestive tract of *T. limbatus* and germinate after being excreted (Lunde et al. [unpublished]). Larvae of *P. ferruginea* develop in decaying wood of various species, typically coniferous trees (Miłkowski et al., 2019). Adults conceal themselves in or near dead wood, e.g. under bark, in hollows, or hiding behind sporocarps (Hågvar, 1999; Miłkowski et al., 2019). *Ipidia binotata* has been identified as a primeval forest relics species in Thüringen, Germany (Weigel & Fritzlar, 2007). Their larvae develop in dead wood, where they feed on mycelium (Horion,

2009). Both *T. limbatus, P. ferruginea* and *I. binotata* can be caught using flight-interception traps during the sporulation period of *F. pinicola* (Gillespie et al., 2017). All three species are associated with both *F. pinicola* fruiting bodies and dead wood, making them likely candidates to disseminate *F. pinicola* spores to suitable substrates where the spores can germinate.

4.4 Conclusions

In this study, I wanted to test the possibility of using time-lapse monitoring of polypores to detect potential fungal spore dispersers on *Fomitopsis pinicola*. I found that time-lapse monitoring has great potential as a method for monitoring insect activity on polypores. However, more work is needed to understand and improve the technique for future ecological studies.

A little more than one third of the images were of high enough quality for the identification of arthropods to be possible. Poor image quality was mainly caused by external factors including condensation and sun glare. The cameras performed better at night, which is also when beetle activity is believed to be highest. However, the flash function, while necessary for night-time monitoring, has the potential to affect beetle behaviour. This was not investigated in this study. No images allowed for detailed taxonomic identification of small beetles, but I was able to identify five large (> 5 mm) and characteristic beetle species. These were *Thymalus limbatus, Ipidia binotata, Lordithon lunulatus, Peltis ferruginea* and *Triplax russica*.

Ecological information about *T. limbatus* activity on *F. pinicola* could be obtained from the image data. The time of day, date, and temperature all had significant effects on *T. limbatus* activity, and the daily activity of *T. limbatus* changed with temperature. *Ipidia binotata* and *L. lunulatus* also exhibited clear temperature preferences. I was also able to estimate the number and duration of visits for *T. limbatus, L. lunulatus* and *I. binotata*. For the other species, the number of observations was insufficient for such estimates to be made.

Mitigating the effects of sun glare and condensation on the lens is likely to improve the overall image quality and enable better recordings of insect visits to polypores in future studies using time-lapse cameras. Although beetles smaller than 5 mm in size are unlikely to be identified to species, this nevertheless provides an efficient method for studying the overall activity and ecology of larger visiting species. Thus, the method can potentially be transferred to other polypore species of which our knowledge is more limited. This will increase our understanding of beetles as potential fungal spore dispersers in dead wood systems.

REFERENCES

Afifi, A., May, S. & Clark, V. A. (2003). *Computer-aided multivariate analysis*: CRC Press.

Akaike, H. (1973). Information theory and the maximum likelihood principle in 2nd International Symposium on Information Theory (BN Petrov and F. Cs ä ki, eds.). *Akademiai Ki à do, Budapest*.

Arjea, J., Miliorisd, D., Tranb, D. T., Jepsene, J. U., Raitoharjub, J., Gabboujb, M., Iosifidisf, A. & Høyea, T. T. (2019). *Automatic Flower Detection and Classification System Using a Light-Weight Convolutional Neural Network*. European Signal Processing Conference 2019.

Aukema, B. H., Clayton, M. K. & Raffa, K. F. (2005). Modeling flight activity and population dynamics of the pine engraver, Ips pini, in the Great Lakes region: effects of weather and predators over short time scales. *Population Ecology*, 47 (1): 61-69.

Azarcoya-Cabiedes, W., Vera-Alfaro, P., Torres-Ruiz, A. & Salas-Rodríguez, J. (2014). Automatic detection of bumblebees using video analysis. *Dyna*, 81 (187): 81-84.

Bader, P., Jansson, S. & Jonsson, B. (1995). Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. *Biological conservation*, 72 (3): 355-362.

Bansal, R., Raj, G. & Choudhury, T. (2016). *Blur image detection using Laplacian operator and Open-CV*. 2016 International Conference System Modeling & Advancement in Research Trends (SMART): IEEE.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.

Birkemoe, T., Jacobsen, R. M., Sverdrup-Thygeson, A. & Biedermann, P. H. (2018). Insect-fungus interactions in dead wood systems. In *Saproxylic Insects*, pp. 377-427: Springer.

Blaser, S., Prati, D., Senn-Irlet, B. & Fischer, M. (2013). Effects of forest management on the diversity of deadwood-inhabiting fungi in Central European forests. *Forest Ecology and management*, 304: 42-48.

Brondizio, E. S., Settele, J., Díaz, S. & Ngo, H. T. (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *IPBES Secretariat*.

Börjesson, T. S., Stöllman, U. M. & Schnürer, J. L. (1993). Off-odorous compounds produced by molds on oatmeal agar: identification and relation to other growth characteristics. *Journal of Agricultural and Food Chemistry*, 41 (11): 2104-2111.

Calhim, S., Halme, P., Petersen, J. H., Læssøe, T., Bässler, C. & Heilmann-Clausen, J. (2018). Fungal spore diversity reflects substrate-specific deposition challenges. *Scientific reports*, 8 (1): 5356.

Castello, J. D., Shaw, C. G. & Furniss, M. (1976). Isolation of Cryptoporus volvatus and Fomes pinicola from Dendroctonus pseudotsugae. *Phytopathology*, 66 (12): 1431-1434.

Chapman, F. M. (1927). Who treads our trails. *National Geographic Magazine*, 52 (3): 330-345.

Dodge, W. E. & Snyder, D. P. (1960). An automatic camera device for recording wildlife activity. *The Journal of Wildlife Management*, 24 (3): 340-342.

Dutta, A. & Zisserman, A. (2019). *The VIA annotation software for images, audio and video*. Proceedings of the 27th ACM International Conference on Multimedia (MM '19), Nice, France. New York, NY, USA: ACM.

Eckelt, A., Müller, J., Bense, U., Brustel, H., Bußler, H., Chittaro, Y., Cizek, L., Frei, A., Holzer, E. & Kadej, M. (2018). "Primeval forest relict beetles" of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants. *Journal of Insect Conservation*, 22 (1): 15-28.

Fernandez, M. A. L., Gelaye, B., Vander Weele, T., Hernandez-Diaz, S., Williams, M. A., Ananth, C., Qui, C., Sanchez, S., Cynthia Ferre, A. M. S.-R. & Holzman, C. (2014). Modelling Time as a Circular Scale.

Floudas, D., Binder, M., Riley, R., Barry, K., Blanchette, R. A., Henrissat, B., Martínez, A. T., Otillar, R., Spatafora, J. W. & Yadav, J. S. (2012). The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science*, 336 (6089): 1715-1719.

Fossil, T.-E. & Andersen, J. (1998). Host preference of Cisidae (Coleoptera) on tree-inhabiting fungi in northern Norway. *Entomologica Fennica*, 9 (2): 65-78.

Fäldt, J., Jonsell, M., Nordlander, G. & Borg-Karlson, A.-K. (1999). Volatiles of bracket fungi Fomitopsis pinicola and Fomes fomentarius and their functions as insect attractants. *Journal of chemical ecology*, 25 (3): 567-590.

Galante, T. E., Horton, T. R. & Swaney, D. P. (2011). 95% of basidiospores fall within 1 m of the cap: a field-and modeling-based study. *Mycologia*, 103 (6): 1175-1183.

George, R. S. (1929). Weather, a factor in outbreaks of the hickory bark beetle. *Journal of Economic Entomology*, 22 (3): 573-580.

Gibb, H., Hjältén, J., P. Ball, J., Atlegrim, O., Pettersson, R. B., Hilszczański, J., Johansson, T. & Danell, K. (2006). Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography*, 29 (2): 191-204.

Gillespie, M. A., Birkemoe, T. & Sverdrup-Thygeson, A. (2017). Interactions between body size, abundance, seasonality, and phenology in forest beetles. *Ecology and evolution*, 7 (4): 1091-1100.

Gomez, A., Diez, G., Salazar, A. & Diaz, A. (2016). *Animal identification in low quality camera-trap images using very deep convolutional neural networks and confidence thresholds*. International symposium on visual computing: Springer.

Guevara, R., Rayner, A. D. & Reynolds, S. E. (2000). Effects of fungivory by two specialist ciid beetles (Octotemnus glabriculus and Cis boleti) on the reproductive fitness of their host fungus, Coriolus versicolor. *New Phytologist*, 145 (1): 137-144.

Haard, R. & Kramer, C. (1970). Periodicity of spore discharge in the Hymenomycetes. *Mycologia*, 62 (6): 1145-1169.

Hackman, W. & Meinander, M. (1979). *Diptera feeding as larvae on macrofungi in Finland*. Annales zoologici fennici: JSTOR.

Halbwachs, H. & Bässler, C. (2015). Gone with the wind–a review on basidiospores of lamellate agarics. *Mycosphere*, 6 (1): 78-112.

Hanski, I. (1989). Fungivory: fungi, insects and ecology. *Insect–fungus interactions*: 25-68.

Harrington, T., Furniss, M. & Shaw, C. G. (1981). Dissemination of hymenomycetes by Dendroctonus pseudotsugae (Coleoptera: Scolytidae). *Phytopathology*, 71 (5): 551-554.

Henderson Jr, C. R. (1982). Analysis of covariance in the mixed model: higher-level, nonhomogeneous, and random regressions. *Biometrics*: 623-640.

Henriksen, S. & Hilmo, O. (2015). Norsk rødliste for arter 2015. *Artsdatabanken, Norge*, 6.

Hobbs, M. T. & Brehme, C. S. (2017). An improved camera trap for amphibians, reptiles, small mammals, and large invertebrates. *PloS one*, 12 (10).

Hoppe, B., Purahong, W., Wubet, T., Kahl, T., Bauhus, J., Arnstadt, T., Hofrichter, M., Buscot, F. & Krüger, D. (2016). Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. *Fungal Diversity*, 77 (1): 367-379.

Horion, N. (2009). Anmerkungen zur Biologie und zum Vorkommen von Ipidia binotata R e it ter, 1875 (Coleoptera, Nitidulidae) sowie Beschreibung der Larven. *Entomologische Nachrichten und Berichte*, 53: 3-4.

Huang, Z.-P., Qi, X.-G., Garber, P. A., Jin, T., Guo, S.-T., Li, S. & Li, B.-G. (2014). The use of camera traps to identify the set of scavengers preying on the carcass of a golden snub-nosed monkey (Rhinopithecus roxellana). *PLoS One*, 9 (2).

Høye, T. T., Arje, J., Bjerge, K., Hansen, O. L., Iosifidis, A., Leese, F., Mann, H., Meissner, K., Melvad, C. & Raitoharju, J. (2020a). Deep learning and computer vision will transform entomology. *bioRxiv*.

Høye, T. T., Mann, H. M. R. & Bjerge, K. (2020b). Kamerabaseret Overvågning af Insekter på Grønne Bytage.

Hågvar, S. & Økland, B. (1997). Saproxylic beetle fauna associated with living sporocarps of Fomitopsis pinicola (Fr.) Karst. In four spruce forests with different management histories. *Fauna Norvegica. Serie B, Norwegian journal of entomology*, 44 (2): 95-105.

Hågvar, S. (1999). Saproxylic beetles visiting living sporocarps of Fomitopsis pinicola and Fomes fomentarius. *Norwegian Journal of Entomology*, 46: 25-32.

Hågvar, S. (2008). Hvor fort vokser knuskkjuke og rødrandkjuke? [How fast do the tinder polypore and the red-banded polypore grow?]. *Blyttia*, 66 (4): 225-230.

Hågvar, S. (2018). Contribution to the ecology of Gyrophaena boleti (Linnaeus, 1758)(Coleoptera, Staphylinidae) breeding in the pore layer of the fungus Fomitopsis pinicola (Fr.) Karst. *Journal of Entomology*, 65: 108-114.

Iredale, S. K., Nevill, C. H. & Lutz, C. K. (2010). The influence of observer presence on baboon (Papio spp.) and rhesus macaque (Macaca mulatta) behavior. *Applied animal behaviour science*, 122 (1): 53-57.

Jacobs, J. M. & Work, T. T. (2012). Linking deadwood-associated beetles and fungi with wood decomposition rates in managed black spruce forests. *Canadian Journal of Forest Research*, 42 (8): 1477-1490.

Jacobsen, R. M., Kauserud, H., Sverdrup-Thygeson, A., Bjorbækmo, M. M. & Birkemoe, T. (2017). Wood-inhabiting insects can function as targeted vectors for decomposer fungi. *Fungal ecology*, 29: 76-84.

Jacobsen, R. M., Sverdrup-Thygeson, A., Kauserud, H. & Birkemoe, T. (2018a). Revealing hidden insect–fungus interactions; moderately specialized, modular and anti-nested detritivore networks. *Proceedings of the Royal Society B: Biological Sciences*, 285 (1876): 20172833.

Jacobsen, R. M., Sverdrup-Thygeson, A., Kauserud, H., Mundra, S. & Birkemoe, T. (2018b). Exclusion of invertebrates influences saprotrophic fungal community and wood decay rate in an experimental field study. *Functional ecology*, 32 (11): 2571-2582.

Johansson, T., Olsson, J., Hjältén, J., Jonsson, B. G. & Ericson, L. (2006). Beetle attraction to sporocarps and wood infected with mycelia of decay fungi in old-growth spruce forests of northern Sweden. *Forest Ecology and Management*, 237 (1-3): 335-341.

Jones, L. L. & Raphael, M. G. (1993). Inexpensive camera systems for detecting martens, fishers, and other animals: guidelines for use and standardization. *Gen. Tech. Rep. PNW-GTR-306. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station. 22 p*, 306.

Jonsell, M. & Nordlander, G. (1995). *Field attraction of Coleoptera to odours of the wood-decaying polypores Fomitopsis pinicola and Fomes fomentarius*. Annales Zoologici Fennici: JSTOR.

Jonsell, M., Nordlander, G. & Ehnström, B. (2001). Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. *Ecological Bulletins*: 173-194.

Jonsell, M. & Nordlander, G. (2004). Host selection patterns in insects breeding in bracket fungi. *Ecological Entomology*, 29 (6): 697-705.

Jonsson, B. G., Siitonen, J. & Stokland, J. N. (2012). The value and future of saproxylic diversity.

Junninen, K. & Komonen, A. (2011). Conservation ecology of boreal polypores: a review. *Biological Conservation*, 144 (1): 11-20.

Kaila, L. (1993). A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. *Entomologica Fennica*, 4 (1): 21-23.

Kaila, L., Martikainen, P., Punttila, P. & Yakovlev, E. (1994). *Saproxylic beetles (Coleoptera) on dead birch trunks decayed by different polypore species*. Annales zoologici fennici: JSTOR.

Komonen, A. (2001). Structure of insect communities inhabiting old-growth forest specialist bracket fungi. *Ecological Entomology*, 26 (1): 63-75.

Komonen, A. (2003). *Distribution and abundance of insect fungivores in the fruiting bodies of Fomitopsis pinicola*. Annales zoologici fennici: JSTOR.

Komonen, A., Jonsell, M., Økland, B., Sverdrup-Thygeson, A. & Thunes, K. (2004). Insect assemblage associated with the polypore Fomitopsis pinicola: a comparison across Fennoscandia. *Entomologica Fennica*, 15 (2): 102–112-102–112.

Komonen, A. (2008). Colonization experiment of fungivorous beetles (Ciidae) in a lake-island system. *Entomol. Tidskr*, 129: 141-145.

Krasutskii, B. (2007). Coleoptera associated with Fomitopsis pinicola (Sw.: Fr.) Karst.(Basidiomycetes, Aphyllophorales) in the forests of the Urals and Transurals. *Entomological Review*, 87 (7): 848-858.

Kucera, T. E. & Barrett, R. H. (1993). In my experience: the Trailmaster® camera system for detecting wildlife. *Wildlife Society Bulletin*: 505-508.

Lachat, T., Wermelinger, B., Gossner, M. M., Bussler, H., Isacsson, G. & Müller, J. (2012). Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. *Ecological Indicators*, 23: 323-331.

Lacy, R. C. (1984). Predictability, toxicity, and trophic niche breadth in fungus-feeding Drosophilidae (Diptera). *Ecological Entomology*, 9 (1): 43-54.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011). Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, 11 (5): 1027-1039.

Lawrence, J. F. (1973). Host preference in ciid beetles (Coleoptera: Ciidae) inhabiting the fruiting bodies of Basidiomycetes in North America. *Bulletin Museum of Comparative Zoology*, 145 (3): 163-212.

Lilleskov, E. A. & Bruns, T. D. (2005). Spore dispersal of a resupinate ectomycorrhizal fungus, Tomentella sublilacina, via soil food webs. *Mycologia*, 97 (4): 762-769.

Lonsdale, D., Pautasso, M. & Holdenrieder, O. (2008). Wood-decaying fungi in the forest: conservation needs and management options. *European Journal of Forest Research*, 127 (1): 1-22.

Mann, H. M., Ärje, J., Iosifidis, A. & Høye, T. T. (2019). *Climate sensitivity of tundra plant-pollinator interactions tracked by computer vision*. Entomology 2019: ESA.

Meek, P. (2012). Refining and improving the use of camera trap technology for wildlife management and research in Australia and New Zealand. *The Winston Churchill Memorial Trust of Australia: Canberra, Australia*.

Meek, P. & Pittet, A. (2013). User-based design specifications for the ultimate camera trap for wildlife research. *Wildlife Research*, 39 (8): 649-660.

Meek, P. D., Fleming, P., Ballard, G., Banks, P., Claridge, A. W., Sanderson, J. & Swann, D. (2014). *Camera trapping: wildlife management and research*, vol. 2: Csiro Publishing Melbourne, Australia:.

Meek, P. D., Ballard, G.-A. & Fleming, P. J. (2015). The pitfalls of wildlife camera trapping as a survey tool in Australia. *Australian Mammalogy*, 37 (1): 13-22.

Meyer, P., Schaffrath, U. & Schmidt, M. (2015). Extinction by forestry? Empirical evidence for decreasing species richness of saproxylic beetles since the 19th century in Hesse (Germany). *Verh. Ges. Ökol*, 45: 165-166.

Miłkowski, M., Tatur-Dytkowski, J., Gutowski, J. M., Ruta, R., Grzywocz, J., Konwerski, S., Królik, R., Kubisz, D., Lasoń, A. & Melke, A. (2019). Trogossitidae, Lophocateridae, Peltidae and Thymalidae (Coleoptera: Cleroidea) of Poland: distribution, biology and conservation. *Polish Journal of Entomology*, 88 (3): 215-274.

Neath, A. A. & Cavanaugh, J. E. (2012). The Bayesian information criterion: background, derivation, and applications. *Wiley Interdisciplinary Reviews: Computational Statistics*, 4 (2): 199-203.

Newey, S., Davidson, P., Nazir, S., Fairhurst, G., Verdicchio, F., Irvine, R. J. & van der Wal, R. (2015). Limitations of recreational camera traps for wildlife management and conservation research: A practitioner's perspective. *Ambio*, 44 (4): 624-635.

Nichols, M., Glen, A. S., Garvey, P. & Ross, J. (2017). A comparison of horizontal versus vertical camera placement to detect feral cats and mustelids. *New Zealand Journal of Ecology*, 41 (1): 145-150.

Norros, V., Penttilä, R., Suominen, M. & Ovaskainen, O. (2012). Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. *Oikos*, 121 (6): 961-974.

Norros, V., Rannik, Ü., Hussein, T., Petäjä, T., Vesala, T. & Ovaskainen, O. (2014). Do small spores disperse further than large spores? *Ecology*, 95 (6): 1612-1621.

Nuss, I. (1982). Die Bedeutung der Proterosporen: Schlußfolgerungen aus Untersuchungen anGanoderma (Basidiomycetes). *Plant systematics and evolution*, 141 (1): 53-79.
Nuss, I. (1986). Zur Ökologie der Porlinge II.
O'Connell, A. F., Nichols, J. D. & Karanth, K. U. (2010). *Camera traps in animal ecology: methods and analyses*: Springer Science & Business Media.
Oneto, D. L., Golan, J., Mazzino, A., Pringle, A. & Seminara, A. (2020). Timing of fungal spore release dictates survival during atmospheric transport. *Proceedings of the National Academy of Sciences*, 117 (10): 5134-5143.
Orledge, G. M. & Reynolds, S. E. (2005). Fungivore host-use groups from cluster analysis: Patterns of utilisation of fungal fruiting bodies by ciid beetles. *Ecological Entomology*, 30 (6): 620-641.
Osztreiher, R. (1995). Influence of the Observer on the Frequency of the 'Morning-Dance'in the Arabian Babbler. *Ethology*, 100 (4): 320-330.
Paviour-Smith, K. (1960). The fruiting-bodies of macrofungi as habitats for beetles of the family Ciidae (Coleoptera). *Oikos*, 11 (1): 43-71.
Peay, K. G. & Bruns, T. D. (2014). Spore dispersal of basidiomycete fungi at the landscape scale is driven by stochastic and deterministic processes and generates variability in plant–fungal interactions. *New Phytologist*, 204 (1): 180-191.
Pech-Pacheco, J. L., Cristóbal, G., Chamorro-Martinez, J. & Fernández-Valdivia, J. (2000). *Diatom autofocusing in brightfield microscopy: a comparative study*. Proceedings 15th International Conference on Pattern Recognition. ICPR-2000: IEEE.
Pegoraro, L., Hidalgo, O., Leitch, I. J., Pellicer, J. & Barlow, S. E. (2020). Automated video monitoring of insect pollinators in the field. *Emerging Topics in Life Sciences*: ETLS20190074.
Pereira, P. H. C., Leal, I. C. S. & de Araújo, M. E. (2016). Observer presence may alter the behaviour of reef fishes associated with coral colonies. *Marine Ecology*, 37 (4): 760-769.
Pettey, T. M. & Shaw, C. G. (1986). Isolation of Fomitopsis pinicola from in-flight bark beetles (Coleoptera: Scolytidae). *Canadian Journal of Botany*, 64 (7): 1507-1509.
Quinn, G. P. & Keough, M. J. (2002). Design and power analysis. In *Experimental design and data analysis for biologists,* pp. 158-172: Cambridge University Press.
R Core Team. (2017). R Core Team (2017). R: A language and environment for statistical computing. *R Found. Stat. Comput. Vienna, Austria. URL http://www.R-project.org/. ,page R Foundation for Statistical Computing*.
Reenskaug, C. (2020). *Biller i Østmarka. Hvordan vernestatus, mengde død ved og skogens åpenhet påvirker billesamfunnet*. Master's thesis. Ås, Norway: Norwegian University of Life Sciences.
Rovero, F., Zimmermann, F., Berzi, D. & Meek, P. (2013). " Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, 24 (2).
Rowcliffe, J. M. & Carbone, C. (2008). Surveys using camera traps: are we looking to a brighter future? *Animal Conservation*, 11 (3): 185-186.
Ryvarden, L. & Melo, I. (2017). Poroid fungi of Europe 2nd edition. Synopsis Fungorum 37. 156.
Schiegg, K. (2000). Effects of dead wood volume and connectivity on saproxylic insect species diversity. *Ecoscience*, 7 (3): 290-298.
Schigel, D. S. (2011). *Polypore—beetle associations in Finland*. Annales Zoologici Fennici: BioOne.
Schigel, D. S. (2012). Fungivory and host associations of Coleoptera: a bibliography and review of research approaches. *Mycology*, 3 (4): 258-272.
Schmid, L., Bässler, C., Schaefer, H. & Krah, F.-S. (2019). A test of camera surveys to study fungus-animal interactions. *Mycoscience*.
Scotson, L., Johnston, L. R., Iannarilli, F., Wearn, O. R., Mohd-Azlan, J., Wong, W. M., Gray, T. N., Dinata, Y., Suzuki, A. & Willard, C. E. (2017). Best practices and software for the management and sharing of camera trap data for small and large scales studies. *Remote Sensing in Ecology and Conservation*, 3 (3): 158-172.

Seibold, S., Müller, J., Baldrian, P., Cadotte, M. W., Šťursová, M., Biedermann, P. H., Krah, F.-S. & Bässler, C. (2019). Fungi associated with beetles dispersing from dead wood–Let's take the beetle bus! *Fungal Ecology*, 39: 100-108.

Shiras, G. (1906). *Photographing wild game with flashlight and camera*: National Geographic Society.

Siitonen, J. (1994). *Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods*. Annales zoologici fennici: JSTOR.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest ecology and management*, 128 (3): 211-225.

Smith, J. K. & Coulson, G. (2012). A comparison of vertical and horizontal camera trap orientations for detection of potoroos and bandicoots. *Australian Mammalogy*, 34 (2): 196-201.

Steen, R., Aase, O. & Thorsdatter, A. L. (2011). Portable digital video surveillance system for monitoring flower-visiting bumblebees. *Journal of Pollination Ecology*, 5.

Steen, R. & Mundal, D. (2013). New video registration of Autographa pulchrina (Haworth, 1809)(Lepidoptera, Noctuidae) and Sphinx pinastri L., 1758 (Lepidoptera, Sphingidae) pollinating Platanthera bifolia latiflora (Orchidaceae) in Norway. *Norwegian Journal of Entomology*, 60 (1): 57-61.

Steen, R. (2017). Diel activity, frequency and visit duration of pollinators in focal plants: in situ automatic camera monitoring and data processing. *Methods in Ecology and Evolution*, 8 (2): 203-213.

Steen, R. & Barmoen, M. (2017). Diel activity of foraging Eurasian red squirrels (Sciurus vulgaris) in the winter revealed by camera traps. *Hystrix*, 28 (1).

Stenlid, J. & Gustafsson, M. (2001). Are rare wood decay fungi threatened by inability to spread? *Ecological bulletins*: 85-91.

Stokland, J. N., Siitonen, J. & Jonsson, B. G. (2012). Introduction. In *Biodiversity in dead wood*: Cambridge university press.

Suetsugu, K., Nakahama, N., Ito, A. & Isagi, Y. (2017). Time-lapse photography reveals the occurrence of unexpected bee-pollination in Calanthe izuinsularis, an endangered orchid endemic to the Izu archipelago. *Journal of Natural History*, 51 (13-14): 783-792.

Talbot, P. (1952). Dispersal of fungus spores by small animals inhabiting wood and bark. *Transactions of the British Mycological Society*, 35 (2): 123-128.

Taylor, B. D., Goldingay, R. L. & Lindsay, J. M. (2014). Horizontal or vertical? Camera trap orientations and recording modes for detecting potoroos, bandicoots and pademelons. *Australian Mammalogy*, 36 (1): 60-66.

Thorn, S., Müller, J., Bässler, C., Gminder, A., Brandl, R. & Heibl, C. (2015). Host abundance, durability, basidiome form and phylogenetic isolation determine fungivore species richness. *Biological journal of the Linnean Society*, 114 (3): 699-708.

Thunes, K. H., Midtgaard, F. & Gjerde, I. (2000). Diversity of coleoptera of the bracket fungus Fomitopsis pinicola in a Norwegian spruce forest. *Biodiversity & Conservation*, 9 (6): 833-852.

Tran, D. T., Høye, T. T., Gabbouj, M. & Iosifidis, A. (2018). *Automatic Flower and Visitor Detection System*. 2018 26th European Signal Processing Conference (EUSIPCO): IEEE.

Tuno, N. (1999). Insect feeding on spores of a bracket fungus, Elfvingia applanata (Pers.) Karst.(Ganodermataceae, Aphyllophorales). *Ecological Research*, 14 (2): 97-103.

Ver Hoef, J. M. & Boveng, P. L. (2007). Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology*, 88 (11): 2766-2772.

Weigel, A. & Fritzlar, F. (2007). „Urwaldrelikte "in Thüringen–Käferarten als Anzeiger für besonders schutzwürdige Wälder. *Landschaftspflege und Naturschutz in Thüringen*, 44 (2): 45-55.

Wiley, M. J. & Kohler, S. L. (1981). An assessment of biological interactions in an epilithic stream community using time-lapse cinematography. *Hydrobiologia*, 78 (2): 183-188.

Yamashita, S., Ando, K., Hoshina, H., Ito, N., Katayama, Y., Kawanabe, M., Maruyama, M. & Itioka, T. (2015). Food web structure of the fungivorous insect community on bracket fungi in a Bornean tropical rain forest. *Ecological entomology*, 40 (4): 390-400.

Zeileis, A., Kleiber, C. & Jackman, S. (2008). Regression models for count data in R. *Journal of statistical software*, 27 (8): 1-25.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*: Springer Science & Business Media.

Økland, B. & Hågvar, S. (1994). The insect fauna associated with carpophores of the fungus Fomitopsis pinicola(Fr.) Karst. in a southern Norwegian spruce forest. *Fauna Norvegica, Series B*, 41 (1): 29-42.

Økland, B., Bakke, A., Hågvar, S. & Kvamme, T. (1996). What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity & Conservation*, 5 (1): 75-100.

APPENDICES

A. Python script – Variance of Laplacian

The Python script used to calculate the VL threshold and sort images into ‘good’ and ‘bad’ directories based on that threshold. The script was provided by Hjalte M.R. Mann and is reproduced here with his permission.

```
# -*- coding: utf-8 -*-
"""
Created on Tue Oct 22 16:51:02 2019

This script calculates the variance of the Laplacian (VL) as a measure for sharpness of an
image for each image in a given directory. The mean and SD is calculated.

The SortImages function sorts images in a given directory on the basis of a threshold
value.

@author: Hjalte Mann
"""
##############
### Import the necessary packages:
import cv2                              # Handling images. This is the openCV package and it
                                        # needs to be installed.
from statistics import mean, pstdev  # Calculate mean and SD
import os                               # Create folders etc.
import shutil                           # Move files
###
##############

##############
### Set paths til the relevant folders:
path_to_good = "C:/Example/Path_good"  # Path to folder with good images (manually
                                       # categorised) from which VL threshold will be
                                       # calculated.
path_to_test = "C:/Example/Path_test"  # Path to folder with images that need to be sorted.
###
##############

##############
### Make an empty list:
blur_good = []  # Make an empty list that will contain the VL's for the good images
###
##############

##############
### Below three different functions are defined:
def variance_of_laplacian(image):
       # Function that computes the Laplacian of the image and then returns the focus
       # measure, which is simply the variance of the Laplacian.
       return cv2.Laplacian(image, cv2.CV_64F).var()

def GetBlurry(path, output_list):
       # Function that loops over the images in a directory, calculates the VL and append
       # the value to a list. The function needs the path to the images (path) and the name
       # of the list to output to (output_list).
       for images in os.listdir(path):  # Loop over images in the given directory
              path_to_image = os.path.join(path, images)  # Set the full path to an image
              image = cv2.imread(path_to_image)               # Load the image
              gray = cv2.cvtColor(image, cv2.COLOR_BGR2GRAY)  # Convert the image to
                                                              # grayscale.
              VL = variance_of_laplacian(gray)  # Calculate VL with the
                                                # variance_of_laplacian-function.
              output_list.append(VL)  # Append the VL value to the output_list
```

```
def SortImages(path):
        # Function that sort images on the basis of their VL and a given threshold.
        sorted_good = os.path.join(path, "sorted_good")  # Create a string with the path for
                                                         # sorted good images.
        sorted_bad  = os.path.join(path, "sorted_bad")   # Create a string with the path for
                                                         # sorted bad images.
        os.mkdir(sorted_good)  # Create the directory (folder) for the sorted_good images in
                               # the test directory.
        os.mkdir(sorted_bad)   # Create the directory (folder) for the sorted_bad images in
                               # the test directory.
        for images in os.listdir(path):  # Loop over images in the direcotry given by "path"
                if images.endswith('.JPG'):  # But only do the rest if the filename ends with
                                             # .JPG (we have just created two folders in the
                                             # test directory and we don't want to include
                                             # these in the next.)
                        path_to_image = os.path.join(path, images)  # Set the full path to the
                                                                    # image.
                        image = cv2.imread(path_to_image)               # Load the image
                        gray = cv2.cvtColor(image, cv2.COLOR_BGR2GRAY)  # Convert the image to
                                                                        # grayscale.
                        VL = variance_of_laplacian(gray)  # Calculate VL with the
                                                          # variance_of_laplacian-function.
                        if VL > threshold:  # If the VL for the image is above the given
                                            # threshold...
                                shutil.move(path_to_image, sorted_good)  # ... then move it to
                                                                         # the sorted_good
                                                                         # folder.
                        if VL < threshold:  # If the VL for the image is below the given
                                            # threshold...
                                shutil.move(path_to_image, sorted_bad)  # ... then move it to
                                                                        # the sorted_bad folder
###
##############

##############
### Now we use our function on our data:
GetBlurry(path_to_good, blur_good)  # Run out GetBlurry-function on the good images. Set
                                    # the output_list to blur_good (the empty list we
                                    # defined earlier in the script).

good_mean = mean(blur_good)         # Calculate the mean VL for the good images
good_sd = pstdev(blur_good)         # Calculate the VL SD for the good images

threshold = good_mean - good_sd     # Set the threshold as VL-SD ( values from good images)

SortImages(path_to_test)    # Run our SortImages function on the images in the test folder.
                            # The function uses the threshold above, which can also just be
                            # set manually (e.g. threshold = 5).
###
##############

##############
### Print some stuff:
print("Mean VL for good: ", good_mean)
print("VL SD for good: ", good_sd)
print("Threshold set to: ", threshold)
print("All done")
###
##############
```

B. Covariates

Table B.1. A list of the covariates that were included in the model selection procedure to find the best GLMM of *Thymalus limbatus* activity on *Fomitopsis pinicola* from time-lapse images taken between May 14th and September 22nd, 2019.

	Covariate	Description
	FIXED EFFECTS	
Temporal variables	Day of year (DOY)	Continuous predictor (134 – 265). 1 = January 1st, 2019.
	Daily oscillation…	Oscillatory transformations from a linear daily covariate (Minute of day, 1 – 1440).
	… (sin 1)	- Single frequency sine function.
	… (cos 1)	- Single frequency cosine function.
Environmental variables	Temperature (°C)	Continuous variable measured with the cameras' internal thermometer.
Site-specific variables	Dead Wood Volume	The estimated volume (*V*) of course woody debris[1] (CWD) within an area of 25m × 25m around the study site. *V* was calculated as $V = \frac{\pi * h * r^2}{3}$, where *h* = height & *r* = radius at breast height. [1] *of diameter >10 cm and length > 1m*
	No. of sporocarps	Number of *F. pinicola* sporocarps within an area of 25m × 25m around the study site.
	Study area	Factor variable w/ four levels (MORT, OST, RAM & SKU)
Statistical interactions		Daily oscillation (cos 1 & sin 1) was tested for interactions with Temperature.
	RANDOM EFFECTS	
Spatial variables	Site ID	Factor variable w/ 11 levels, corresponding to study site (MORT1, MORT2, MORT3, etc.)

C. Examples – bad images

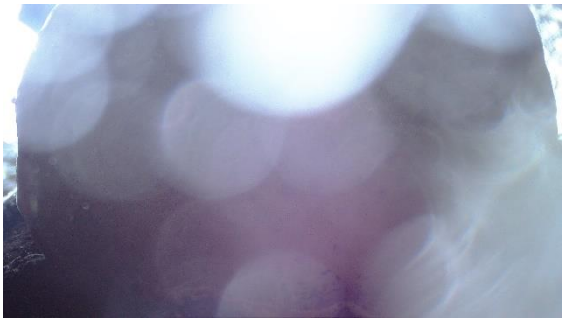


Figure C.1. Poor quality due to sun glare and dew.

Figure C.2. Poor quality due to overexposure.

Figure C.3. Poor quality due to sun glare.

Figure C.4. Poor quality due to condensation or fog.

Figure C.5. Poor quality due to rain.

D. Examples – beetle visitors

Figure D.1. *Ipidia binotata*, OST2, June 14th.

Figure D.2. *Lordithon lunulatus*, RAM1, June 15th.

Figure D.3. *Triplax russica*, MORT3, June 10th.

Figure D.4. Unidentified beetle, RAM2, August 28th.

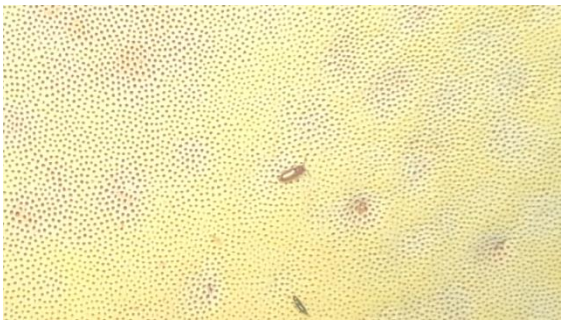


Figure D.5. Unidentified beetle, MORT1, June 9th.

E. Number of good images per study site and per day

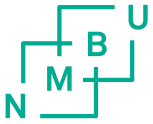
The frequency of good images per study site for each individual date with at least one active camera, for each of the two periods when cameras were active (May 14th, 2019 – June 19th, 2019 on this page; July 31st, 1019 – September 22nd, 2019 on the next page). NA (marked in grey) signifies that the camera was not active on that day, typically because the camera had not been placed out yet or because it turned itself off during fieldwork (e.g. because the battery had run out). Cells are coloured in a gradient from red to white, with 0s being filled in with the darkest shade of red.

Table E.1. Frequency of good images per site and per day from May 14th to June 19th, 2019.

MORT1	MORT2	MORT3	OST1	OST2	OST3	RAM1	RAM2	RAM3	SKU1	SKU2	
NA	NA	NA	NA	NA	NA	48	54	64	NA	NA	14.05.2019
NA	NA	NA	NA	NA	NA	144	144	24	NA	NA	15.05.2019
NA	NA	NA	NA	NA	NA	144	140	NA	NA	NA	16.05.2019
NA	NA	NA	NA	NA	NA	84	63	NA	NA	NA	17.05.2019
35	43	47	NA	NA	NA	47	45	NA	NA	NA	18.05.2019
108	35	54	NA	NA	NA	37	43	NA	NA	NA	19.05.2019
76	0	53	NA	NA	NA	0	22	NA	NA	NA	20.05.2019
82	0	55	62	59	26	11	7	NA	NA	NA	21.05.2019
39	0	47	52	49	2	0	36	NA	NA	NA	22.05.2019
55	0	45	46	76	0	21	51	NA	75	NA	23.05.2019
62	0	30	28	66	0	23	31	NA	47	NA	24.05.2019
16	0	25	12	21	0	0	8	NA	0	NA	25.05.2019
26	3	45	14	36	19	0	33	NA	0	NA	26.05.2019
52	0	41	48	58	34	0	32	NA	0	47	27.05.2019
36	0	24	NA	2	0	0	33	NA	0	127	28.05.2019
94	18	22	NA	1	0	34	19	NA	68	45	29.05.2019
50	0	51	NA	9	0	45	34	NA	52	9	30.05.2019
31	0	40	NA	0	0	29	32	NA	52	0	31.05.2019
0	0	10	NA	0	0	0	30	NA	36	0	01.06.2019
0	0	5	NA	47	40	0	24	NA	3	0	02.06.2019
0	0	11	NA	139	50	12	20	NA	30	46	03.06.2019
62	61	85	NA	136	64	124	126	NA	115	91	04.06.2019
115	130	132	NA	128	33	74	68	NA	129	53	05.06.2019
106	113	123	NA	111	25	89	110	NA	123	31	06.06.2019
35	78	97	NA	95	13	11	29	NA	41	0	07.06.2019
52	79	121	NA	83	0	37	12	NA	55	1	08.06.2019
94	54	103	NA	85	1	23	9	NA	40	0	09.06.2019
144	111	143	NA	143	11	105	8	NA	39	0	10.06.2019
137	109	133	NA	140	2	123	21	NA	43	0	11.06.2019
76	61	114	NA	35	3	25	7	NA	43	0	12.06.2019
117	46	115	NA	51	15	42	13	NA	59	0	13.06.2019
40	87	108	NA	67	19	67	10	NA	66	0	14.06.2019
86	119	131	NA	127	77	144	42	NA	142	0	15.06.2019
56	141	144	NA	144	41	132	103	NA	137	0	16.06.2019
54	136	143	NA	141	75	143	142	NA	142	0	17.06.2019
42	144	144	NA	144	24	143	144	NA	144	0	18.06.2019
26	104	109	NA	119	2	91	88	NA	79	0	19.06.2019

Table E.2. Frequency of good images per site and per day from June 31st to Sept. 22nd, 2019.

MORT1	MORT2	MORT3	OST1	OST2	OST3	RAM1	RAM2	RAM3	SKU1	SKU2	
24	53	51	NA	0	NA	NA	14	NA	61	0	31.07.2019
107	133	144	NA	0	NA	NA	97	NA	141	3	01.08.2019
142	139	141	NA	0	NA	NA	96	NA	140	5	02.08.2019
124	140	144	NA	0	NA	NA	111	90	141	46	03.08.2019
44	120	59	NA	0	NA	NA	49	46	97	2	04.08.2019
51	99	44	NA	0	NA	NA	64	50	99	5	05.08.2019
41	127	130	NA	0	NA	NA	67	48	128	0	06.08.2019
31	143	125	NA	4	NA	NA	104	69	136	0	07.08.2019
77	140	144	NA	144	NA	NA	114	50	144	1	08.08.2019
56	139	126	NA	118	NA	NA	125	107	142	2	09.08.2019
46	68	54	NA	124	NA	NA	42	21	97	2	10.08.2019
4	3	40	NA	31	NA	NA	19	NA	73	0	11.08.2019
28	41	74	NA	4	NA	NA	66	NA	77	0	12.08.2019
2	40	44	NA	41	NA	NA	119	NA	68	0	13.08.2019
20	12	65	NA	65	NA	NA	106	NA	61	0	14.08.2019
53	44	86	NA	71	NA	NA	119	NA	70	0	15.08.2019
1	83	71	NA	144	NA	NA	100	NA	127	0	16.08.2019
10	86	54	NA	70	NA	NA	38	NA	90	0	17.08.2019
0	93	81	NA	68	NA	NA	66	NA	102	0	18.08.2019
7	22	60	NA	20	NA	NA	44	NA	74	0	19.08.2019
3	41	80	NA	9	NA	NA	88	NA	98	0	20.08.2019
3	83	125	NA	57	NA	NA	122	NA	113	0	21.08.2019
3	94	99	NA	59	NA	NA	85	NA	106	0	22.08.2019
2	31	68	NA	9	NA	NA	87	NA	51	0	23.08.2019
17	14	116	NA	53	NA	NA	133	NA	NA	0	24.08.2019
0	0	93	NA	31	NA	NA	117	NA	NA	0	25.08.2019
0	5	112	NA	0	NA	NA	94	NA	NA	0	26.08.2019
0	28	89	NA	8	NA	NA	144	NA	NA	0	27.08.2019
0	0	55	NA	1	NA	NA	59	NA	NA	0	28.08.2019
0	11	54	NA	2	NA	NA	65	NA	NA	0	29.08.2019
0	7	47	NA	0	NA	NA	30	NA	NA	0	30.08.2019
0	34	51	NA	0	NA	NA	41	NA	NA	0	31.08.2019
0	13	51	NA	0	NA	NA	25	NA	NA	0	01.09.2019
0	65	124	NA	2	NA	NA	65	NA	NA	0	02.09.2019
0	13	88	NA	0	NA	NA	37	NA	NA	0	03.09.2019
0	12	40	NA	0	NA	NA	1	NA	NA	0	04.09.2019
0	32	53	NA	0	NA	NA	21	NA	NA	0	05.09.2019
0	39	12	NA	0	NA	NA	39	NA	NA	NA	06.09.2019
0	18	4	NA	0	NA	NA	0	NA	NA	NA	07.09.2019
0	0	57	NA	0	NA	NA	17	NA	NA	NA	08.09.2019
0	0	50	NA	0	NA	NA	31	NA	NA	NA	09.09.2019
0	0	52	NA	0	NA	NA	0	NA	NA	NA	10.09.2019
0	0	32	NA	0	NA	NA	0	NA	NA	NA	11.09.2019
0	NA	43	NA	0	NA	NA	NA	NA	NA	NA	12.09.2019
1	NA	126	NA	0	NA	NA	NA	NA	NA	NA	13.09.2019
0	NA	93	NA	0	NA	NA	NA	NA	NA	NA	14.09.2019
0	NA	111	NA	0	NA	NA	NA	NA	NA	NA	15.09.2019
0	NA	128	NA	0	NA	NA	NA	NA	NA	NA	16.09.2019
1	NA	122	NA	2	NA	NA	NA	NA	NA	NA	17.09.2019
0	NA	126	NA	21	NA	NA	NA	NA	NA	NA	18.09.2019
0	NA	125	NA	14	NA	NA	NA	NA	NA	NA	19.09.2019
0	NA	110	NA	23	NA	NA	NA	NA	NA	NA	20.09.2019
1	NA	125	NA	59	NA	NA	NA	NA	NA	NA	21.09.2019
0	NA	67	NA	4	NA	NA	NA	NA	NA	NA	22.09.2019



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