Exploring the impacts of microclimatic temperature on occupancy of the Apollo butterfly (*Parnassius apollo*)

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Master's thesis

Climate driven environmental conditions and division of resources have a key role in determining the distribution of ecosystems and organisms. Ongoing anthropogenic climate change has already enabled some species to expand their distribution or limits the range of others. Species living in northern latitudes and mountainous habitats are especially vulnerable to the effects of climate change and it's challenging their capability to adapt. Recent studies have shown that microclimates may buffer the effects of climate change by providing thermal niches, where the species are able to persist. Butterflies, such as the study species *Parnassius apollo*, is one of the groups most affected by the temperature rise. Their habitat selection, life cycle, and survival are often dependent on thermal conditions. Furthermore, both ambient temperature and microclimatic variation can affect ovipositing behavior of butterflies. The decline of *P. apollo* has been rapid in recent decades, and the reasons behind it are still largely unknown. In my study, I investigate if the species occupancy is related to temperature differences of the available habitat patches. Furthermore, I examine if the larvae distribution within habitat patch is impacted by the small-scale thermal variation. I deployed temperature loggers on 35 rocky outcrops within the known distribution area of *P. apollo* in Parainen, SW Finland. Detailed census, including survey of larvae occupancy and abundance, and host plant (*H. telephium*) count, was carried out on all patches in spring 2020. In addition to above, total of 18 temperature loggers (6 on each) were deployed on three selected habitat patches to investigate the small-scale thermal variation of the occupied patches. I found out that the habitat patches occupied by *P. apollo* are warmer than the unoccupied ones, both when comparing mean and minimum temperatures of larvae period (29.4.-15.6.) and wing-time (1.7.-15.8.). No difference in maximum temperatures was found. Based on my results, the spring mean and summer minimum temperatures are the temperature variables with the biggest effect on occupancy and larvae abundance. Moreover, there was no significant difference in the number or density of host plants between occupied or unoccupied patches. However, the occupied patches were larger. When inspecting the small-scale thermal variation of occupied patches, the maximum temperatures were higher in cells with larvae and host plant than in cells with just host plant growing only on one patch. Yet, also when inspecting other locations and variables, the larvae were mostly found from warmer cells ($p > 0,05$). Even though, the earlier studies suggest that the host plant abundance is the major factor determining the occupancy of *P. apollo*, my study shows that microclimatic temperature variation may impact the occupancy and larvae abundance. Further studies are needed to investigate the role of microclimatic conditions on *P. apollo* occupancy and distribution. Furthermore, I suggest that habitat heterogeneity should be considered when implementing habitat restoration measures, in order to preserve thermal variation on the habitat patches.

Contents

1. Introduction

1.1. The role of microclimates in ecology

Climate has a major effect on biotic communities and ecosystems of the Earth by determining the division of conditions and resources, and their interaction. Environmental factors, driven by the solar radiation and consequently by climate, play a key role in defining the distribution of ecosystems and organisms. Together with local factors, such as soil type and topography, the world's climate has resulted in global characteristic terrestrial vegetation regions, called biomes. The biomes are mostly resulting from the variation of temperature and precipitation. The definition of main biomes has varied through the history and between biogeographers. Often main terrestrial biomes of the world are divided to 8-10 biomes. Main biomes include e.g. boreal forests, temperate forests, deserts and mountains. Even though most biomes can be found from all continents, and share the same characteristics, it's important to acknowledge that their evolutionary and genetic history differ. Moreover, the boundaries of biomes are indistinct, and they include large number of habitats differing from each other. (Begon et al. 1990, 5-7, 9-14, 26-28; Monteith & Unsworth 2013; Begon et al. 2014, 92-111)

It's indisputable that the climate has an essential role in determining the patterns, composition and diversity of ecosystems and organisms, both in global and regional scale. However, in ecological perspective, the global climate is often only setting the boundaries of conditions and resources, and hence the localized climatic conditions near land's surface, together with its properties, creates the actual local climate, often called microclimate. (Rotach & Calanca 2003; Mislan & Helmuth 2008; Zellweger et al. 2019) In ecology, the definition of microclimate is highly dependent on the objective and question addressed. Moreover, the concept of microclimate can include variety of variables depending on the aims and focus of the study. When addressing microclimatic conditions, the commonly measured environmental variables are temperature, humidity, light and humidity. Yet, both the variable and the scale vary according to the studied habitat or organism. For example, in landscape ecology, the microclimate can be measured on a scale of tens or even hundreds

of kilometers, while investigating the microclimate meaningful for animals or plants, the scale can vary from meters to even centimeters. Thus, in ecology the definition of microclimate is often determined by the habitats or species in concern. (Rotach & Calanca 2003; Mislan & Helmuth 2008; Suggitt et al., 2011; Bramer et al. 2018; Zellweger et al. 2019; Lembrechts & Lenoir, 2020) Furthermore, microclimatic small-scale thermal variations, are often resulted by the changes in vegetation and topography of the terrain that inflicts thermal gradients within the landscape (Rosenberg, 1974; Suggitt et al 2011).

Microclimate is meaningful to organisms in many ways since it greatly dictates the environmental conditions where organisms can live. Moreover, it affects to the resource availability through the whole food chain by affecting the production. In most cases microclimatic conditions, such as temperature, humidity, and light, limit the distribution of organism by inducing physiochemical responses. The response depends on the variable concerned. In extreme temperature conditions, too cold or hot are lethal, but moreover temperature may have an effect to growth, survival, and reproduction of organisms. Consequently, temperature is often the main limiting factor of species distribution, and species-specific optimal temperature, also called as thermal niche, can be defined for most species. Often, the thermal niche is used or included when modelling the species distribution. Usually, organisms are separated to two types when examining their relationship to temperature, endotherms, and ectotherms (also homeotherms and poikilotherms) (Begon et al. 1990, 48-51; Begon et al. 2014, 64-67). Endotherms include organisms that can control their body temperature by producing heat within their bodies, whereas ectotherms temperature is dependent to heat sources of their environment. Simplified, the endotherms consist of mammals and birds and ectotherms include reptiles, invertebrates, and fish. Yet, few exceptions occur. (Begon et al. 1990, 48-51; Begon et al. 2014, 64-67)

It is increasingly important to understand the role of microclimates for different species if we want to understand the consequences of ongoing anthropogenic change in climate. Even thought, the ongoing increase of ambient temperature may diminish the range of species in large scale, the environmental heterogeneity may provide microclimatic niches where the species are still able to persist. Thus, the microclimates may have a significant role in buffering the effects of climate change. (Keppel et al. 2012; Potter et al., 2013; Isaak et al. 2017; Maclean et al. 2015; Pincebourde et al. 2019; Zellweger et al. 2020; De Frenne et al.

2021) This highlights our need to understand what's the role of microclimates for different species. In other words, how the thermal variation effects to their survival, reproduction, and range, and consequently how this may affect the species' population dynamics and demography. However, in order to examine the effects of temperature on species-specific and ecologically meaningful scale, we need adequate and accurate data. (Patten et al. 2012; Isaak et al. 2017; De Frenne et al. 2019; De Frenne et al. 2021) In recent years, the importance of microclimate conditions in ecology has increased, and its relevance has been acknowledged. (Suggitt et al. 2011; Lembrechts & Lenoir 2020) Due to this, also the need of critical evaluation of methodology and available data has increased. (Lembrechts et al. 2019; Zellweger et al. 2019a; Maclean et al. 2021) As mentioned above, the definition of microclimate in ecology is highly dependent on the objective of the study and examined organism. Therefore, the methods and approaches may vary significantly, and the availability of accurate and ecologically relevant data can be a challenge. Moreover, the monitoring of environmental variables, even as simple as temperature, may be challenging for ecologists if the monitoring design and setup isn't well thought out and assessed. Maclean et al. (2020) addressed this topic in their study, by evaluating different devices and shields used for temperature measurements in ecological studies. Study also included the device used in this study, iButton Thermocron. The study underlies the importance and need of reliable and accurate microclimatic temperature data if we want to understand the interaction of organisms and their habitat. (Maclean et al. 2021)

1.2. Microclimatic conditions and butterflies

As all insects, the butterflies are ectotherms, and thus their body temperature is determined and controlled by external heat sources, such as direct sunlight or surface temperatures. (Berwaerts et al. 2001; Bryant et al. 2002; Kemp & Krockenberg 2004). Moreover, some activities e.g. flight, are highly dependent on heat. This makes them highly sensitive to climatic changes and limitations. (Dennis & Shreeve 1991; Bryant et al. 2002). Consequently, the distribution range and occurrence of butterflies is often limited by climate and temporal variation of temperatures. Often latitude or altitude determines the climatic tolerance of butterfly species in broad scale. (Dennis & Shreeve 1991; Gutierrez & Menendez 1995; Dennis et al. 2008) The main reason for this is that the climate sets the

timely restrictions, and boundary conditions to the completion of the life cycle of butterflies (Thomas 1993; Oliver et al. 2009). Due to climate change, the distribution of many species has expanded, and increased temperatures have caused changes in the timing and duration of occurrence (Sparks et al. 2006; Lawson et al. 2012). Furthermore, increased temperatures have resulted changes in the dispersal behavior (Sparks et al. 2005, Sparks et al. 2007). When discussing the effects of climate change on species distribution, it's important to acknowledge that climate change is also a significant driver of habitat loss and fragmentation, and hence influences species distribution in multiple, and in some cases in opposite ways (Mantyka-Pringle et al. 2012).

The importance of thermal heterogeneity of habitats and role of microclimates for butterflies has been shown in many studies. (e.g., Thomas 1993; Ashton et al. 2009; Bennett et al. 2014; Checa et al. 2014; Curtis et al. 2015; Suggitt et al. 2015; Stuhldeher & Fartmann 2018). Also, the studies have proven that the small-scale thermal variation may affect butterflies in many ways. Braby & Jones (1994) showed that larval development rate was linked to the temperature of a host plant. Furthermore, studies have shown that the selection of ovipositing site can be affected by temperature variation. (Roy & Thomas 2003; Dennis 2010). Often, the role of thermal conditions is highlighted for the populations inhabiting the high latitudes of the species distribution area (e.g. Ashton et al. 2009). In his studies, Thomas (Thomas 1993, 1995; Thomas et al. 2002) showed that at the northern range, butterflies survived because they inhabited patches that were in earlier successional stage, and hence more open and warmer, than the members of the same species living in more southern range. Consequently, the populations living at northern range are more limited by microclimatic niches.

Studies have also revealed that especially in Northern Europe, the number of suitable microclimates and their connectivity affects the abundance of many butterflies (Thomas et al. 2001; Krämer et al. 2012; Eilers et al. 2013). Yet, the role of temperature driven changes (climate change) on occupancy, abundance and populations dynamics are still poorly known (Davies et al. 2006; Turlure et al. 2010). Often the studies emphasize the urgent need to understand these temperature driven changes, and moreover the question if the habitat quality or microclimatic temperature, is a more notable predictor of species distribution and abundance. This is a vital question for conservation management and functional habitat restoration. (Roy & Thomas 2003; Curtis et al. 2015)

Environmental conditions, such as temperature and precipitation, also drive metapopulation dynamics. (Hanski & Meyke 2005; Ojanen et al. 2013) For the Glanville fritillary butterfly (*Melitaea cinxia*), the withering of host plants, due to high temperatures, resulted starvation of larvae and historically low size of the metapopulation in 2010 (Ojanen et al. 2013). The Glanville fritillary has been the model species when developing the metapopulation theory (Hanski et al. 2005). Curtis & Isaak (2015) investigated on microhabitat scale, the role of microclimatic conditions and habitat quality, to see which is better predictor of the abundance variation of the Glanville fritillary. The data consisted of both local and regional temperature data gathered from one population. Also, the surface temperatures of plants used for ovipositing were recorded. The study revealed that temporal changes in habitat quality, and ambient air temperature both determined the abundance of the Glanville fritillary butterfly. Moreover, they found out that the female butterflies more likely oviposit on host plants which temperatures were significantly higher than the ambient temperature. Based on the results Curtis & Isaak (2015) concluded that the annual changes in abundance are linked with the amount of host plants growing in suitable microclimates. Furthermore, this explains why the populations in northern range have large annual fluctuations. In warmer years, the Glanville fritillary females are more likely to utilize host plants growing in cooler microclimatic niches. Based on the results, they recommend that management practices should be targeted to create thermally heterogenous habitats which serve more options to female butterflies to oviposit and are able to buffer the effects of annual variations in temperature. Results support the fact that microclimates have an essential role in buffering the effects of climate change on species distribution and abundance of butterflies. Furthermore, the study corroborates the importance of microscale habitats by conserving the thermal variation, and moreover the need of maintaining these habitats in order to populations to cope with the increasing temperature fluctuations in future (New 2009; Curtis et al 2015; Morecroft 2012).

1.3. The endangered Apollo butterfly

The Apollo butterfly (*Parnassius apollo, Linnaeus 1758, family Papilionidae*) is a threatened species in Finland with IUCN status endangered (EN) (Hyvärinen et al. 2019) and is mentioned in annex IV of Habitats Directive and in Appendix II by the Convention

on International Trade in Endangered Species of Wild Fauna and Flora (EU Council 1992). In Finland it has been protected by law since 1976. The biggest reason for conservation concern of the Apollo butterfly, is the drastic decline in distribution during the twentieth century. In Finland the decline has been rapid. Until the 1950's the distribution used to cover the whole southern and central part of the country, however currently Apollos may be found only from few fragmented areas in southern and southwestern part of Finland. (Mikkola 1979; Huldén et al. 2000) Recent study by Kukkonen et al. (2022) confirms that the decline of *P. apollo* has been extreme and rapid, at least in the population living in the outer archipelago zone of the Archipelago Sea. Furthermore, distribution decline has been reported throughout the Europe, and local extinctions has occurred in few countries (van Swaay & Warren 1999; Nakonieczny et al. 2007).

In the most part of its distribution area *P. apollo* is an alpine species and its caterpillar feeds on Sedum species. In Finland, the distribution is restricted in relation of main host plant *Hylotelephium telephium*. Yet, Apollos are absent in large areas in southern and southeast Finland, where the host plant occurs. Currently Apollos occur only on a narrow coastal region and archipelago area with suitable habitat. Suitable habitat consists of rocky agricultural areas in coastal area and inner archipelago and barren treeless islands in the outer archipelago, where the host plant grows on rocky outcrops. (Brommer & Fred 1999; Fred 2004; Fred & Brommer 2015) In agricultural and forested areas, suitable habitat patches, outcrops with *H. telephium*, can be relatively small, yet in the archipelago an entire island may form a suitable habitat patch. Based on the studies by Fred M. & Brommer J. E. the populations in the inner archipelago can be considered patchy, thus dispersal is common between the habitat patches, and from the patches to areas with nectar plants. Whereas in the outer archipelago the distance between habitat patches can be long and dispersal between patches is seldom. Thus, an island or group of islands close to each other, may form a metapopulation. (Brommer, & Fred 1999; Fred 2004).

Although several studies have been carried out, the causes of the decline are still largely unknown; weakening and disappearing of habitats, heavy metals together with acid rains, climate change, diseases and illegal collection, are all named as possible reasons of the decline. Also, joint effects may occur. (e.g. Sanchez-Rodrıguez & Baz 1996; Nieminen et al. 2001; Fred & Brommer 2005; Nakonieczny et. al 2007; Boitier et al. 2008; Keba et al. 2021). In Finland, several studies, e.g. on the influence of habitat quality, host plant

abundance and importance of nectar resources, on population structure and dynamics has been carried between late 90's – the present (e.g. Fred & Brommer 2003, Fred et al. 2006; Fred & Brommer 2015). In addition, ovipositing behavior of female has been examined since it may have an essential role on the population dynamics (Fred & Brommer 2003, 2010). Studies have shown that typically the female Apollo butterflies don't lay their eggs on the host plant (Fred & Brommer 2003; Ashton et al. 2009) Yet, the ovipositing behavior may differ between populations, i. e. depending on the host plant species and density (Wiklund 1984; Fred & Brommer 2003).

The study carried out by Fred & Brommer (2003) in outer archipelago population (SW Finland), discovered that the female *P. apollo* doesn't oviposit directly on the host plant but lays single eggs to the surroundings of host plants. The median distance to the nearest host plant was 4 meters. Yet, the study also showed that the ovipositing isn't totally random even though it may look like it, and thus the host plant abundance is crucial for larval survival. It needs to be noted that on these investigated small islands, the density of host plant (*H. telephium*) is often high. Similar ovipositing behavior has been recorded in other populations, but also ovipositing directly on host plants occurs (Wiklund 1984; Ashton et al. 2009; Fred & Brommer 2010). In the inner archipelago population (Parainen), study area of this work, female Apollos have been observed to oviposit both randomly on moss and lichen, and directly on the host plant in recent years. (pers. obs. Laaksonlaita) Behavior is similar that has been described by the Clouded Apollo (*Parnassius mnemosyne*) (Wiklund 1984; Konvicka & Kuras 1999). In butterflies in general, ovipositing off the host plant randomly isn't unusual, especially for species overwintering as an egg but usually it occurs when the host plant of the species is very abundant. Also, studies have shown, that some species which ostensibly place their eggs randomly, have very strict microclimatic requirements on the ovipositing place (Salz & Fartmann 2009) or they prefer ovipositing locations that are warmer than their surroundings (Curtis & Isaak 2015).

As mentioned above, in most parts of its range *P. apollo* inhabits mountainous regions that are vulnerable to the changes caused by climate change (also Keba et al. 2021). Descimon et al. (2005) showed that at the low elevations of the alpine habitats, the decline of *P. apollo* is most likely connected to the warming of climate. Since the effect of increased temperature on the species range and abundance is likely, few studies focusing on the impact of temperature on habitat use and range has been carried out (Ashton et al. 2009;

Wilson et al. 2014). Even though the studies are focused on mountainous region situated in Spain, where the warming is resulting range shifts towards higher elevations (Wilson et al. 2014), the findings may be applicable also in the northern margin range of *P. apollo*. Ashton et al. (2009) discovered that fine-scale microclimatic temperature variation may play are a significant role through thermoregulation of larvae. Ground cover heterogeneity, i.e. variation of bare ground, host plants and other vegetation, can either provide the larvae opportunity to sun-basking or shelter during too hot or too cold periods. In the higher elevations larvae preferred microhabitats with more bare ground and lower surrounding vegetation which suggested that larvae favored hotter conditions. Furthermore, with microclimatic temperature measurements, Ashton et al. (2009) found out that larval microhabitat occupancy was related to the ambient temperature. If the ambient temperature exceeded 27°C, larvae preferred more shaded microhabitats, cooler than the ambient temperature, whereas in cooler conditions larvae preferred more open habitats. In their study, Wilson et al. (2014) found out that larvae occupancy could be negatively linked to the slope direction. They suspected that this is likely to be a result from so called "false-spring" events. In springtime sudden warming may cause emergence of larvae in the southern slopes, and this may result higher mortality when the cold weather returns. False-spring events have most likely resulted declines of *P. apollo* in some regions, and they are becoming more common due to climate change (Descimon et al. 2005; Schmeller et al. 2011). Unexpectedly, Wilson et al. (2014) didn't find any evidence that the decline would be greater in lower elevations, presumably caused by warming climate. Both studies highlighted the role of habitat variability, connectivity and local microclimates, so that the local populations may persist the climatic variation caused by climate change. When local extinctions occur, it is essential to maintain suitable larvae habitats and habitat connectivity to enable colonization of *P. apollo* (Brommer & Fred, 1999; Fred et al. 2006; Ashton et al. 2014; Keba et al. 2021). Since the climate change will have severe impacts on climate (drought, rainfall), which may consequently weaken the habitat suitability and even effect the population dynamics of *P. apollo*, my study could provide an important baseline information on the temperature conditions of the habitat patches of the population in concern (Kahilainen et al. 2018).

1.4. Study aims and hypothesis

The original hypothesis and the aims of the study are based on assumption that the microclimatic conditions, and thus habitat suitability, has changed within the Parainen distribution area. The assumption is founded on the knowledge gathered nearly 20 years ago from the same area (e.g. Brommer & Fred 1999; Fred 2004) and the surveys conducted by myself and other voluntary within recent years. It's evident that the decline of *P. apollo* is drastic in Parainen and the reasons behind the decline are largely unknown (Fred & Brommer 2005). Since the thermal variation and microclimates are known to be a significant driver of abundance and distribution for many butterflies (e.g. Thomas et al. 2001; Krämer et al. 2012; Eilers et al. 2013; Ojanen et al. 2013; Curtis & Isaak 2015), I came up with an idea to investigate the impact of microclimatic temperature on the occupancy of *P. apollo* in the Parainen distribution area. Studies have also shown that some species which ostensibly place their eggs randomly, have very strict microclimatic requirements on the ovipositing place (Salz & Fartmann 2009), and furthermore species laying their eggs on host plant, prefer ovipositing locations that are warmer than their surroundings (Curtis & Isaak 2015).

1) Study aims to investigate the differences in microclimatic temperature between habitat patches, and its relation to occupancy. Study hypothesis that the habitat patches occupied by *P. apollo* are warmer and more sunbaked, and hence the overgrowth of habitat patches and shading following from it, may weaken the habitat suitability or even make it totally unsuitable for the species, even though the host plants still occur on the patch and their abundance haven't decreased notably.

2) As a continuation to above, detailed microclimatic temperature variation in relation to fine-scale distribution of larvae will be examined within three selected habitat patches. I originally hypothesized that microclimatic thermal variation may influence the selection of ovipositing locations of *P. apollo.* In other words, females lay their eggs in certain microclimatic niches, and the ovipositing isn't close-to-random even though it may ostensibly look like it. However, it can't be excluded that the small-scale thermal variation may also affect the survival of eggs and larvae during winter and early spring, since I wasn't able to record the exact ovipositing locations. Thus, this part of my study aims to

examine if there's a pattern between appearance of small larvae and small-scale thermal niches, which can be a consequence of either ovipositing or survival.

2. Material and methods

2.1. Study species

Parnassius apollo is one of the largest butterflies occurring in Finland with a wingspan ranging from 65 up to 95 mm. *P. apollo* has white wings with characteristic 4-5 black spots and grey markings, and two eye-catching bright red or orange spots in the hindwings. (Figure 1) (Higgins & Riley 1980; Collins & Morris 1985; Marttila et al. 1991; Haahtela et al. 2011; Silvonen et al. 2014)

Figure 1. Apollo butterfly has white wings with characteristic black and grey markings and bright red spots in its hindwings.

The distribution area of *P. apollo* covers a large area from the western Europe all the way to central Asia. However, it's an alpine species within most of its distribution area, and often occurs sparsely and in low numbers. (Higgins & Riley 1980; Marttila et al. 1991) In Finland, it can be only found from the archipelago of the Archipelago Sea and Åland islands. Furthermore, a small and isolated population lives in inland of southern Finland in

Uusimaa region. (Figure 2) (Marttila et al. 1991; Silvonen et al. 2014). Besides Finland it only occurs on lower altitudes in Sweden in the island of Gotland.

The wing-time of *P. apollo* takes place from the beginning of July until mid-August. In some years adult butterflies can be seen in flight already in the end of June. During their wing-time adult Apollo's feed mainly on large nectar flowers, such as thistles (*Cirsium*), brown knapweed (*Centaurea jacea*), rosebay willowherb (*Epilobium angustifolium*) and common valerian (*Valeriana officinalis*). (Fred 2004; Fred et al. 2006)
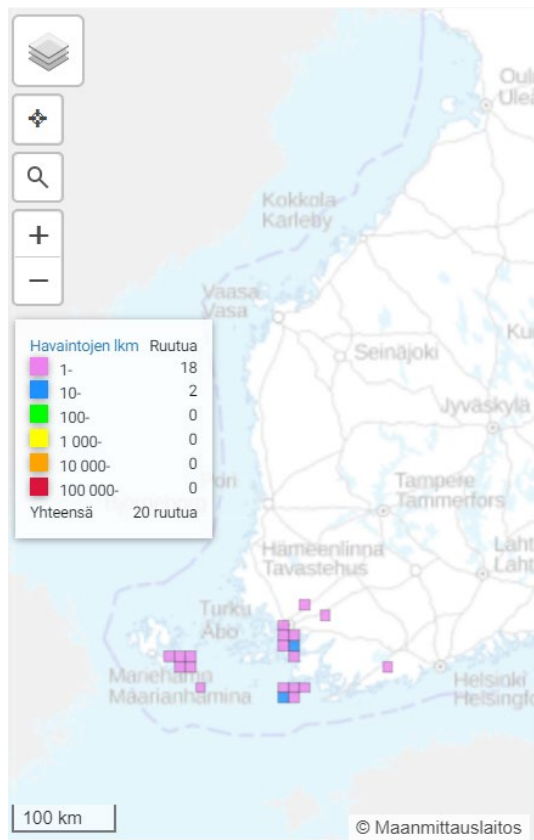
Figure 2. Recorded P. apollo observations in Finland after 2010. Map gives a good image of the current distribution of Apollo butterfly in Finland. Map includes only observations by experts and sightings made by proficient enthusiasts that are confirmed by an expert. The inland observations situated north from Turku are most likely a result of illegal translocation. (Suomen lajitietokeskus 2023)

As well as the adult butterflies, also the larvae of *P. apollo* are easily recognizable and hard to mix with other species. First after hatching the small larvae are dull black, but soon as they grow, humps with red-orange colorization appear on their sides. This colorization is known to act as defensive mechanism and warning coloration to forewarn the possible

predators. (Tolman & Lewington 1997) In Finland, larvae hatch between late April and early May, and directly start feeding on their host plant. Due to the early time of the year larvae mostly feed during warm and sunny days and can then be seen on host plant or sun-basking next to it. The black colorization may have an important role for the heat absorbance, and hence thermoregulation which is particularly interesting for this study. During colder periods larvae are often passive and hide within the undergrowth. (Marttila et al. 1991; Fred & Brommer 2003; Bohlin et al. 2008; Ashton et al. 2009) Furthermore, they can even prevent themselves freezing by chemical substances (Marttila et al. 1991).

Figure 3. Left: Larvae feeding on an orpine plant (*Hylotelephium telephium*). Right: When not feeding, the larvae often hide in lichen or moss close to the host plant.

In Finland, the only host plant for *P. apollo* is the orpine plant or livelong (*Hylotelephium telephium*, family of Crassulaceae). In other populations *P. apollo* also feed on other *Sedum* species, such as white stonecrop (*Sedum album*). *H. telephium* is a perennial plant which range covers large areas in temperate climate regions of Europe and Asia. Moreover, it's found from parts of the North America, where it's an invasive species. *H. telephium* grows typically on nutrient poor, dry and rocky habitats, and is sensitive to overgrowth and eutrophication. (Piirainen et al. 1999; Kontula & Raunio 2018; Hyvärinen et al. 2019) In Southern Finland the species is commonly found from rocky forested outcrops and rocky meadows, shores, and rocky islets in the archipelago. The distribution is mainly limited to the coastal areas and southwest parts of the country. (Piirainen et al. 1999) In its habitats, the *H. telephium* is one of the earliest species to sprout in the spring, after snow has melt and temperatures begin to rise. Since the orpine plant is the sole host plant of Apollo, its occurrence and density are crucial factors for the occupancy and larvae survival of *P. apollo* (Brommer & Fred 1999; Fred & Brommer 2003, 2010). Therefore, also the

relationship of microclimatic temperature and occurrence of *H. telephium* is interesting. Moreover, temperature and precipitation may affect to sprouting time and survival of the of *H. telephium*. Thus, fluctuations of temperatures may lead to imbalance between occurrence time of the host plant and larvae. Furthermore, in case of an extreme drought in spring, the shoots of orpine can wither prematurely hindering the larvae to finalize their development (Ashton et al. 2009; pers. obs. Laaksonlaita). In the parts of its range, where *P. apollo* uses multiple host plants (Sedum spp.) it may enhance survival of larvae if the host plants are affected by drought during the larval period (Ashton et al. 2009).

2.2. Study area

The study area is situated in southwest Finland, in the city of Parainen (Figure 5). Area is one of the last strongholds of Apollo butterfly in Finland apart from populations living in the outer archipelago of the Archipelago Sea and Åland islands (Fred & Brommer 2004).

Area is situated in inner archipelago of the Archipelago Sea, about 15km south from the city of Turku (Figure 5). Area consists of large, forested islands, narrow and shallow straits and eutrophicated bays. The landscape is characterized by modern cultivated landscape, with fields and settlements, and small-scale forested areas, where groves, coniferous forest and rocky outcrops alternate. Parainen is known of its large lime quarry, and the effect of lime fallout from the quarry can be seen in the species occurring in the area. (Suomen talousseura 1978; Varsinais-Suomen ELY-keskus 2013; Nurmio 2022)

Figure 4. Typical habitat of the P. apollo in Parainen consists of outcrops and rocky meadows.
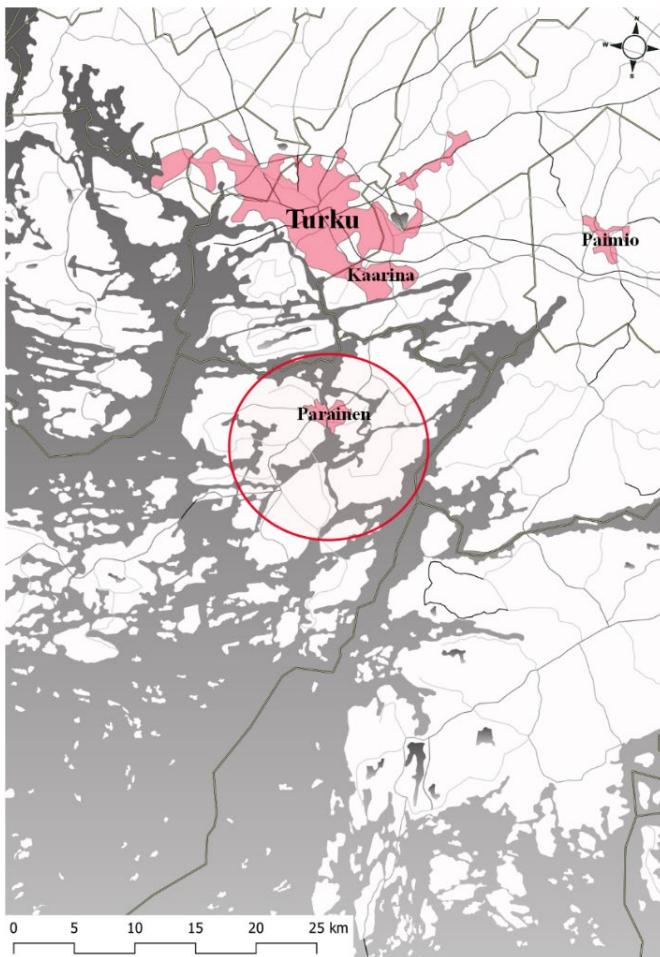
Figure 5. The study area (red circle) is situated in Parainen, 15-25 kilometers south from the city of Turku (SW Finland). Area consists of large, forested islands, and is located in the inner archipelago of the Archipelago Sea.

In the area of Parainen, the *P. apollo* inhabits outcrops in forests on rocky terrain and dry rocky meadows growing the *H. telephium*) (Figure 4). Adult butterflies move between the outcrops and nectar plant patches. Commonly, the nectar plants grow on road and field edges, deforested areas, and small meadows within agricultural areas. Occasionally, nectar plants, such as thistles and brown knapweed (*Centaurea jacea*) also occur in the rocky areas, close to breeding grounds of *P. apollo*. (Brommer & Fred 1999; Fred 2004; Fred et al. 2006)

2.3. Microclimatic temperature data

2.3.1. Used devices and setup

I collected the temperature data by using Thermocron iButton temperature loggers (later Thermocron or temperature logger). Thermocrons are rugged and small, button-like loggers that measure and store the temperatures to internal memory. (Figure 6) These affordable and easy to use loggers can be used for multiple purposes and doesn't require any kind of calibration prior to use.

Thermocrons are widely used for both research and commercial purposes, e.g., for monitoring transportation and room temperatures in food industry (Frank et al. 2019). In research they are utilized for wide range of purposes, from ecology (Kanda et al. 2005; Kinahan et al. 2007; Bennett et al. 2014; Fawcett et al. 2019; Machekano et al. 2019) and animal physiology (Dadgar et al. 2010; Gür et al. 2013; McMaster & Downs 2013) to medicine (Hasselberg et al. 2010; Langer & Fietz 2014; Gericke et al. 2022) and climatic and other environmental monitoring (e.g. Brabyn et al. 2013). Since they are such widely used, the reliability, accuracy, and weaknesses of iButton Thermocrons and similar sensors has been investigated (Wolaver & Sharp 2007; Willis et al. 2009; Hasselberg et al. 2010; Roznick & Alford 2012; Maclean et al. 2021).

Maclean et al. (2021) tested the iButtons with different setups and conditions. They found out that Thermocrons can be sensitive to emitted heat from the ground in sunny conditions, and hence not the best option if used for examining differences between microclimate and

surrounding macroclimate (e.g. weather station data). However, when investigating temperature differences of similar habitats, with similar shading conditions, they are adequate to use. Furthermore, study concluded that low-cost consumer grade temperature loggers, such as iButton Thermocron, are suitable for most ecological settings and purposes, especially when spatial replication is needed, and number of measurement positions is high. In these circumstances they provide reasonable, low-cost, accurate enough and user-friendly option. (Maclean et al. 2021). Based on the studies on iButton Thermocrons or similar devices, and their potential pitfalls and weaknesses in measuring microclimatic temperature, it's justified to say that they are practical solutions to measure the temperature differences of habitat patches of *P. apollo*. Especially, since the emitting heat from the ground and rock can perceived as meaningful factor of microclimate for the species.

Figure 6. iButton Thermocron temperature loggers are small (diameter 18mm) and rugged temperature loggers suitable for multiple purposes.

For the study I used iButton Thermocron model DS1921G which has an operating range from -40°C up to +85°C. The logger has built-in real time clock and accuracy of ±1°C from -30°C to +70°C. Thermocron loggers can be operated with 1-Wire software provided by the manufacturer. Connection to the logger setup and data download is taken simply with interface cable. The logger has sealing level of IP56, yet totally waterproof enclosure is available as an accessory. Thermocron DS1921G can store up to 2048 recordings, with

uniformly pitched intervals ranging from 1 minute up to 255 minutes. (Maxim Integrated 2022)

Every Thermocron logger was tested before the actual deployment. Prior the test the real time clocks were synchronized with PC and 1-Wire software provided by the manufacturer. At the same every tested logger was given a unique ID (1-112). Furthermore, logger's serial-number was taken down to ensure the traceability. Test period was carried out in room temperature. During the test period recordings were relatively stable and loggers took measurements on a set interval. Only one logger failed to work during the test, and thus was put aside. Moreover, test recordings varied within 1-2°C which can be kept allowable, since they were mostly inside the given accuracy of the device and the test conditions weren't standardized. Yet, in case of device failure and to minimize the effect of device dependent deviation in the measurements, I decided to deploy two Thermocrons per site and use the mean of the recordings of these two loggers. This also enabled the use of data from a single logger in the case of potential failure.

After the test, I selected 70 loggers to be deployed to the 35 habitat patches. In the study, habitat patch refers to rocky outcrops visible (grey) on a base map. Similar definition has been used in previous studies (Brommer & Fred 1999; Fred 2004) Again, before the deployment the loggers were connected via 1-Wire software, and the real-time clocks were checked. Also, the loggers were set to measure temperature every half hour (at o'clock sharp and at half past). In order to get the measurement, start and interval synchronized, the delayed start option was used. Time to start can be set in minutes when doing the setup for the logger. When doing the setup, serial number and ID of the device, date and time of the setup, sample rate (minutes), time to start (min) and expected start date and time were written down.
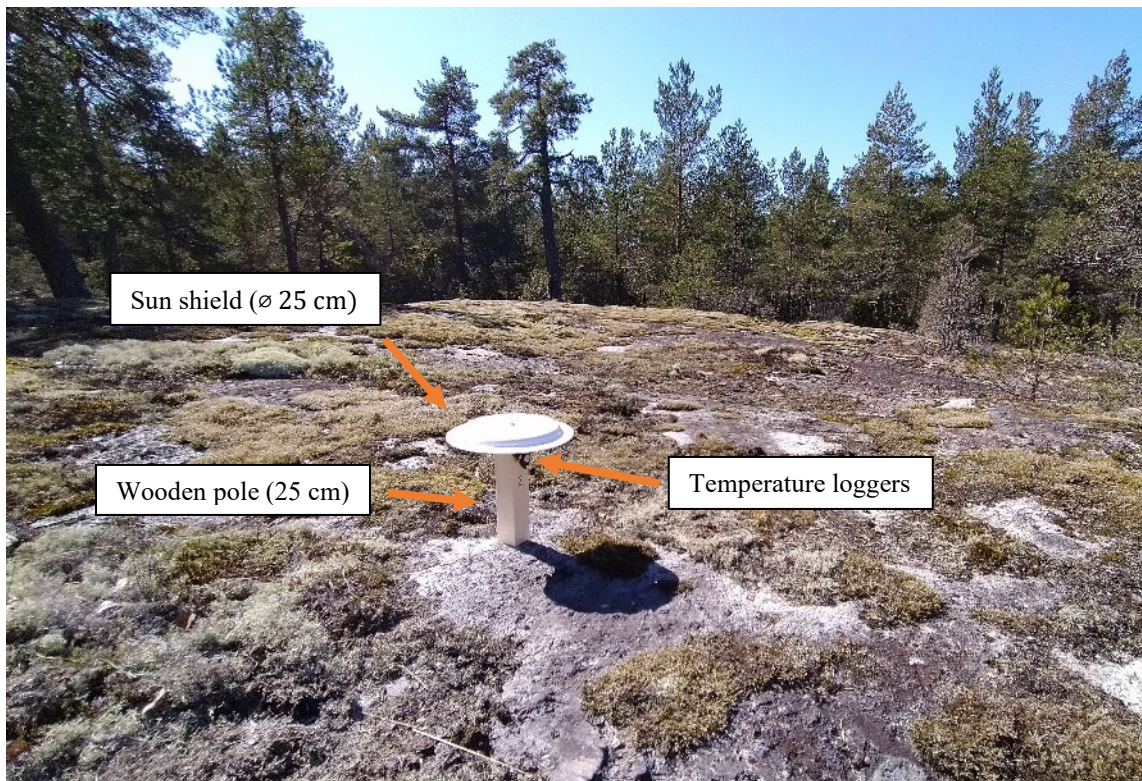
Figure 7. Temperature loggers deployed on a rocky outcrop (= habitat patch). Two Thermocrons were attached 20 cm above ground on a 25cm high wooden pole mounted to the rock. Plastic plate (⌀ 25cm) protects the loggers from the direct sunlight.

Temperature loggers were deployed between 23rd and 28th of April 2020. Loggers were mounted to an angular 25 centimeters high wooden pole. (Figure 7) I mounted the Thermocrons to the pole by using plastic fixing piece which can be attached with screws and keeps the logger in place. As said, for each site two loggers were deployed. Loggers were attached cornerwise as next to each other on the height of 20 centimeters above the ground. The wooden pole was mounted with a ribbed bar, drilled, and fastened with glue to the rock. This was done to make sure that the wooden pole won't turn during the installation period. White plastic plate with diameter of 25 cm was attached to the top of wooden pole, to minimize the effect of direct sunlight, and thus standardize its possible effect to the measurements (Figure 7). Similar setup has been used in previous microclimate studies, and with similar or close to similar temperature loggers (e.g., Bennett et al. 2014; Curtis & Isaak 2015; Löffler & Fartmann 2017; Stuhldeher & Fartmann 2018; Maclean et al. 2020). Furthermore, the loggers were deployed facing north by using a

compass. The direction of loggers was checked every time when the site was visited for census or data download.

Thermocron temperature loggers have a circular memory, thus I downloaded the data approximately once a month until the end of measurement period. When downloading the data, I checked the real-time clocks and set them again if needed. Typically, real-time clocks were slow for 0 to 60 seconds, at maximum 304 seconds. Loggers were taken out from the field between 12th of August and 19th of September. When disassembling the loggers, also the wooden poles and other parts of the setup were taken out from the nature.

As the deployment sites are rocky and sunbaked outcrops it was acknowledged that the radiating heat from the rock will most likely affect the temperature recordings, since the loggers were deployed so near the ground level. However, it was thought that the heat radiation can be considered relevant factor for the microclimate of the habitat patch, and thus also ecologically significant. Furthermore, the deployment height is more less like the height of the host plant of *P. apollo*, which makes it justified especially for the purposes of the aim 2 of this study.

2.3.2. Data collection and measurement design

To investigate the differences in microclimatic conditions between rocky outcrops, and its relation to patch occupancy and habitat preference (aim 1) the temperature was measured on 35 separate sites (habitat patches). In the study, the site refers to rocky outcrop presumably suitable as a habitat patch, and which is situated within the known local distribution area in Parainen area.

As the study required permanent deployment of research devices and their attachments to the rock, permissions from the landowners were consequently required. For the practical reasons I asked the permissions from four great landowners within the study area. Fortunately, these areas are well distributed covering almost all the known distribution area of *P. apollo* in Parainen. Moreover, as the areas are situated on three different island and are 5-10 kilometers apart from each other they most likely represent three or four sub-populations currently living in Parainen distribution area. Sites were situated on islands of Lemlahdensaari (18 loggers), Stortervolandet (12 loggers) and Kirjalansaari (5 loggers).

Roughly loggers distributed on an area of total of 6,25km² (Lemlahdensaari 4,65km², Stortervolandet 1,3 km² and Kirjalansaari 0,3km²). (Figure 8)
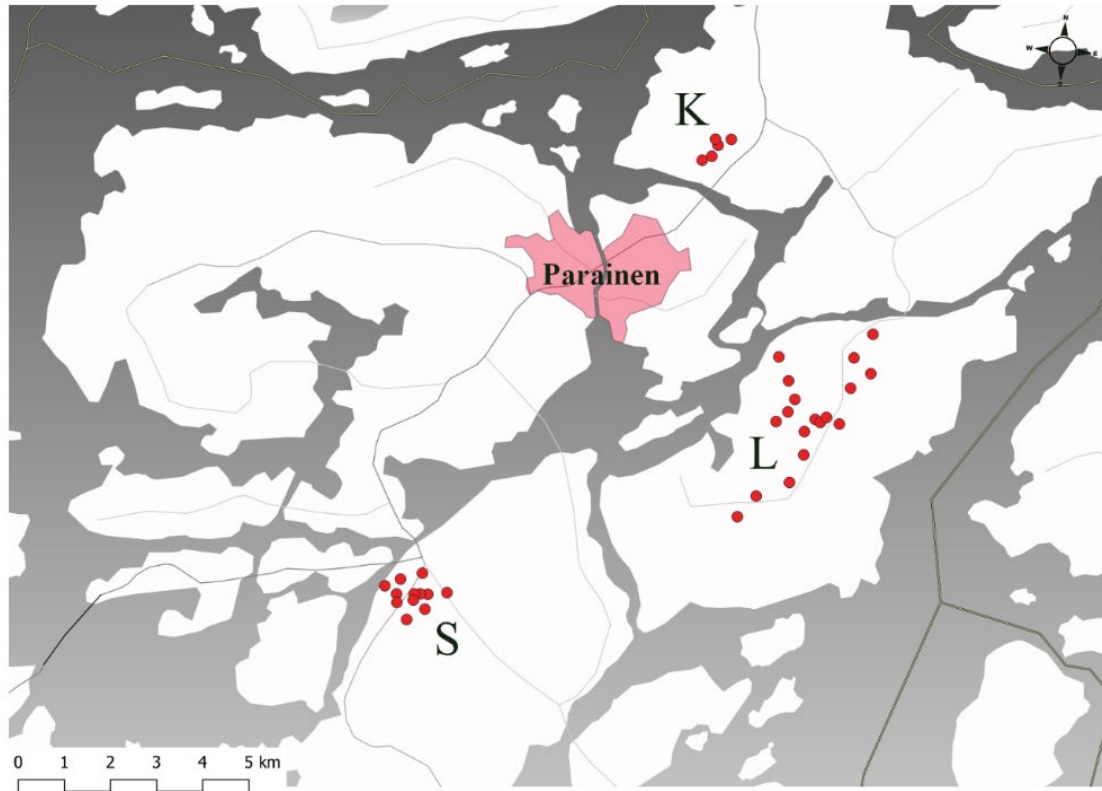
Figure 8. Temperature loggers were deployed on three different islands (K = Kirjalansaari, L = Lemlahdensaari, S = Stortervolandet). The study area covers well the known range of *P. apollo* in Parainen.

Previous studies have been carried out in the same area situated in northwest part of island of Stortervolandet (S). Marianne Fred and Jon Brommer carried out series of studies and censuses on Apollo butterfly between the years 1996 and 2003 (e.g. Brommer & Fred 1999; Fred 2004). Since I was able to get the data on *P. apollo* occupancy and host plant abundance of those six studied years, I decided to carry out the census on the same exact habitat patches (outcrops), but also use part of them as a study site for the microclimatic measurements. I decided to select 12 of the total 35 deployment sites within this area. The microclimate measurement sites were selected so that they represented both occupied and not occupied habitat patches discovered in the 20-year-old studies. From the other parts of the study area, I didn't have any detailed prior or historical knowledge of the occupancy of *P. apollo*.

The selection of specific deployment spot of temperature logger wasn't pre-determined but was done randomly on-site. Nevertheless, I placed the loggers subjectively to the most open part of the outcrop, and in addition facing out the main direction of the patch, and therefore spots are considered to be representative to the patches' microclimatic temperature conditions. It wasn't justified to place loggers randomly to the outcrops, since then they could have been placed to a shaded part of the patch or to the opposite side compared to main direction of the patch, which might have affected the recordings significantly (Maclean et al. 2021) Thus, the measurements wouldn't represent the sites microclimatic temperature and would make comparison questionable. Moreover, all 35 loggers were deployed on bare rock, to minimize the possible variation caused by the groundcover to the comparison of temperature readings.

I recorded additional descriptive information of the site patch main direction, average tree height around the outcrop and possible nectar plants, when doing the deployment and maintenance visit. This additional information can be used in further analysis. Especially, the patch main direction may be significant factor affecting the microclimatic temperature. In my study, the patch main direction refers to the direction where the patch opens, i. e. where it's the most affected by sun. Often also the slope of the outcrop is directed to the same direction. The patch main direction varied from 110° to 325°, and the mean direction was 205 and median 200 degrees. (Figure 9). Since the direction 180° stands for south, and southwest is 225 degrees, most of the patches directed to the sun for the warmest hours of the day. Furthermore, it needs to be noted that the possible shading and patch direction were considered when selecting the specific deployment positions in the field.
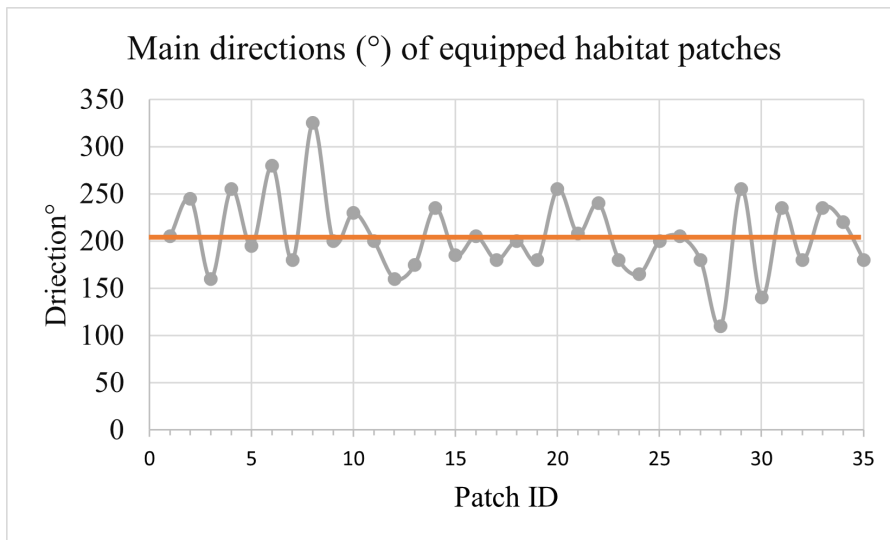
Figure 9. Main directions of the patches where temperature loggers were deployed was recorded. Directions varied from 110 to 325 degrees. Mean direction is marked with the orange line. South = 180°, southwest = 225°.

To answer the questions set in for the aim 2 of the study, I selected three occupied habitat patches on the grounds of the larvae census. All selected patches situated on the island of Lemlahdensaari, relatively near to each other. This was partly because of practical reasons, and partly because most of the occupied patches situated within this area. Later, the selected patches with multiple temperature loggers will be referred with "M1", "M2" and M3".

Selected patches were relatively different from each other. The site M1 was situated on southern slope a relatively steep, high and open rocky outcrop, whereas the M2 was on a small and low outcrop which was surrounded with tick and rich grass-herb vegetation. Site M3 was situated in the middle of few years old clear-cut and the outcrop was exposed to sun from almost all directions. From each of these patches at least one small larvae (< 1 cm) were found during the census. Sizes of the outcrop were 0,16 ha, 0,5 ha and 2,8 hectares. Yet, the largest patch is mostly tree covered and the size of open area is approx. 0,4 hectares, and hence the selected patches can be considered close to similar in size. Each selected patch was equipped with six temperature loggers (18 in total). Loggers were deployed to all the patches on 12nd of June.

Figure 10. Picture from the patch "M3". The patch was situated in the middle of a few years old clear-cut, yet there were few trees growing on the outcrop. You can see three temperature loggers in the picture (red circles).

For the deployment of the loggers to these patches, I used 5 x 2 meters grid (10 x 10m). Thus, the grid consisted of cells of 2 x 2 meters (25 cells). Selected grid and cell size were considered to be relevant for both microclimate and host plant growth form and density, but also functional in relation to the size of the habitat patches. As the aim was to investigate if the small-scale thermal variation affects the larvae distribution within the patch, both the grid and temperature loggers were placed randomly so that the loggers were placed in cells with just host plant and both host plants and larvae. I carried out the randomization on site, by choosing the position of the cell with larvae simply by using Google random number generator. In case of multiple larvae occurred, the randomization was done by using the position of just one of them. After this I marked two sides and corner of the grid to the terrain with 20 meters rope. Additionally, I positioned the grid to direction from south to north. After defining the corner of the grid, I was able to mark down cells with host plant and no host plant. I used tape measure to ease the positioning of cells. This was followed by

choosing the 3-5 cells out all possible, where I then placed the temperature loggers. Number of cells including host plant varied from 8 to 21. As in the earlier stage, the selection was again done by using the random number generator. If there were larvae in several cells, temperature loggers were placed all of these. The larvae count varied between 1-3 in the grids. (Table 1, Figure 11) The actual deployment and mounting of loggers were done in a similar way than described above for the study aim 1 (Figure 7).

Table 1. Number of temperature loggers, cells including larvae and host plants within each grid.

	M1	M2	M3
N of temperature loggers per grid	6	6	6
Cells with larvae and host plant	3	1	2
Cells with host plant	16	20	8
Total number of cells	25	25	25
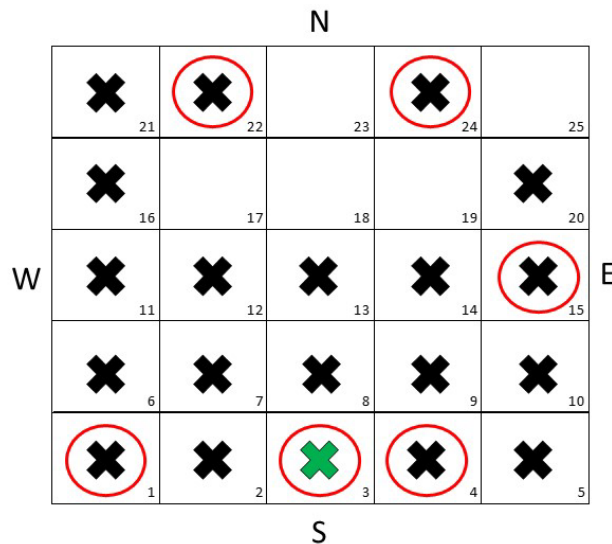
Figure 11. Example of the setup of temperature loggers (location "M2"). Cells with black crosses are the ones with a host plant, and the green cross shows the cell holding both the larvae and host plant. Temperature loggers were deployed to the cells marked with red circles. Selection of equipped cells and the positioning of the grid was done by using random number generator in the field.

2.4. Census

In the spring 2020 I carried out an extensive census in the Parainen distribution area. Survey was carried out with the support of the Centre for Economic Development, Transport and the Environment of Southwest Finland. Census consisted of survey total of 182 rocky outcrops. As mentioned earlier, the habitat patch refers to rocky outcrop marked

on the base map. Similar definition of habitat patches has been used in earlier larvae censuses conducted in the same area (Brommer & Fred 1999; Fred 2004). Data was collected to gain knowledge of the occupancy, abundance and distribution, both *P. apollo* and its host plant, *H. telephium*. As extensive survey has never carried out in Parainen distribution area, thus it provided valuable information of the status of Apollo butterfly in the inner archipelago. Furthermore, the data collected during the census was used for the objectives of this study.

The census was carried out between 5th of May and 17th of June. The early spring of 2020 was cold, and the start of census was decided after first larvae sighting in the end of April. Nevertheless, the start of census can be considered early, yet it was justified because of the extent of the survey area. Nevertheless, I decided to repeat the surveys in later spring of all patches where larvae weren't found during first census and the first census was done before 12th of May. The number of host plants was recorded only on the first time.

Surveys were conducted on all outcrops equipped with temperature loggers. I surveyed them during the regular (extensive) census, and when visiting the sites for the data download. Data was first downloaded between 20th of May and 1st of June. Thus, the download visits were well-timed regarding the count of larvae. The visits for the regular census were carried out 1-3 weeks apart from the visits done because of the data download. All habitat patches equipped with temperature loggers where censused several times (minimum two) during their measurement period.

During the actual census I surveyed all the studied outcrops by myself. Time spent on each outcrop was dependent on the size of it and the amount of host plants. The size of the outcrops surveyed for the study varied from 0,02 to 9,28 hectares (Table 3), and the average size was 2,07 hectares. Since the size and shape and other characteristics of the outcrops vary significantly, any systematic surveying method wasn't appropriate to use. I simply surveyed the outcrops by walking it through systematically and covering its whole area. Similar method has been used also the in earlier studies (e.g., Brommer & Fred 1999; Fred 2007; Kukkonen 2021) This was done by taking the terrain into account. Furthermore, the effort and accuracy of surveying was adapted to the terrain and vegetation of the outcrop. In few cases the outcrop, or parts of it, were totally overgrown, and thus unsuitable for habitat of *P. apollo* and weren't surveyed. This is considered when calculating host plant densities

for the outcrops. Furthermore, I mapped the areas where host plants grew if they were distinctly concentrated to some parts of the surveyed area. This was the case especially with some of the larger rocky outcrops.

During the survey, every outcrop was given an ID and date, start and end time and weather conditions were recorded. Weather observations included temperature, cloudiness (0-7) and rain (y/n). Also, I wrote down if the weather was windy, or clearly cooled down by it. Additionally, I recorded comments on nectar plants, other *Lepidoptera* species, ants, and grazing marks by deer in host plants. For the study species, I recorded the number of larvae, feeding marks and number of *H. telephium*. Host plant count was based on the number of stems. This differs from some of the earlier studies where n of *H. telephium* count has been based on the whole plants. (Kukkonen 2021; Kukkonen personal communication). In these studies, group of five stems have been recorded as a one plant, yet also separately growing stems have been recorded as a plant. However, because of the extent of my study this method would have been more time consuming and secondly, in the study area the *H. telephium* often grows in small groups of only 1-3 stems. Moreover, as the host plant densities are often low within the survey area the single stem can be considered as meaningful unit for *P. apollo*. Similar style of counting *H. telephium* has been used also in other studies in recent years. If the host plant doesn't grow in a dense tuft, also single stems are counted as whole plants. Furthermore, a plant can consist of three or five stems based on its growth type. Method can be combined with the method described above, where a plant is categorically considered to consists of five stems. (Kukkonen & Mussaari 2022; Mussaari personal communication). If using this method, good and clear instructions and competent surveyors are emphasized.

2.5. Statistical analysis

To compare the temperature differences of occupied and unoccupied habitat patches I used independent samples t-test. The comparison was done separately for mean, maximum and minimum temperatures derived from the raw data. The tests were carried out by using IBM SPSS Statistics software (ver. 28.0.1.0.). The independent samples t-test is often used for comparing the means of two independent groups. (Ross & Willson 2017; Gerald 2018) In

addition to temperature variables I checked if there's difference in the patch size of occupied and unoccupied patches since this may be relevant for further analysis.

The effects of microclimatic temperature variables on occupancy of *P. apollo* were contrasted by performing generalized linear model (GLM) by using GLIMMIX procedure in SAS (SAS Enterprise Guide 8.3). The GLIMMIX enables the use of generalized linear mixed models, where response variable is predicted by using both class and fixed factors. Furthermore, it's also possible to include random effects to the model. With the GLIMMIX one can also examine the interactions of factors. (Kiernan 2018; Science Direct 2023a) I carried out the model by using only fixed factors (Table 4), since the collected variables didn't include class factors that would have been justified to use in the model.

I carried several models using different temperature variables factors and their combinations. Since the number of observations is relatively low, I used Akaike's information criterion for sample size AIC_c (Burnham & Anderson 2002) for model evaluation. When using AIC_c value, the model with the lowest value is considered the most parsimonious explanation of observations. In general, the AIC (Akaike's information criterion) is widely used and accepted tool for used for statistical model evaluation. AIC gives an estimation of model's likelihood and enables to assess the models. In principle, the lower AIC value indicates better model fit. (Cavanaugh & Neath 2019; Science Direct 2023b) Furthermore, I inspected the possibility of model overdispersion by comparing Pearson Chi-Square / DF value given by the model result output. Value should be close to one, higher values tell that there's a risk of overdispersion in the used model. Values over 1,5 increase the risk of overdispersion considerably. Overdispersion can be used for comparing the different distributions for the model. Overdispersion is common when using Poisson distribution, commonly used for ecological data.

Prior to carrying out GLM models, I checked if there's a correlation between minimum and mean temperatures by using simple correlation matrix with Proc corr procedure in SAS. Surprisingly, the correlation of mean and minimum temperatures was low (0,158-0,551), and thus it's well-founded to include them in the same model. However, the correlations of mean and minimum temperatures of the same patch from spring and summer were strong, 0,738-0,887. (Table 5) Variables with pair-wise correlation weren't included in the same GLM model. Furthermore, due to limited number of observations (degrees of freedom), too

complicated model wouldn't have given adequate results or no results at all, and thus I didn't include any interactions to the tested models.

3. Results

3.1. The impact of microclimatic temperature on occupancy of *P. apollo*

3.1.1. Occupancy of *P. apollo* in the monitored habitat patches

As described above, the temperature loggers were deployed to 35 habitat patches and all these patches were censused at least two times. The number of occupied patches was 14, and thus 21 of the patches were found not occupied during the census. It needs to be noted that 12 of occupied patches were in Lemlahdensaari, and only one patch was occupied both in Stortervolandet and in Kirjalansaari (Figure 8).

Total number of larvae found was 35, mean number of larvae per patch was 1 and maximum count of larvae for a single patch was 5. (Table 2) When looking at the host plant the maximum number of stems for a single patch was 1003, and the mean number was 183,6 stems. On two outcrops the host plants were absent, thus it can be considered unsuitable for *P. apollo*, and excluded when computing naïve occupancy. Thus, the naïve occupancy for all monitored patches is 0,42 (n = 33). However, if inspecting the occupancy for each island separately, there's large differences. For Stortervolandet the naïve occupancy is only 0,08 (n = 12, occupied = 1), for Kirjalansaari 0,25 (n = 4, occupied = 1) and for Lemlahdensaari as high as 0,63 (n = 18, occupied = 12). Since the study focuses on the temperature differences in relation to the occupancy, further occupancy models aren't computed.

Table 2. Basic information of the census. Total number of censused patches was 182, and the temperature loggers were deployed on 35 patches. Naïve occupancy for the whole census was 0,45 (n = 164) and for the patches with temperature loggers 0,42 (n = 33). The patches with no host plants were not included when calculating the naïve occupancy, since the naïve occupancy (naïve est.) is calculated by dividing the number of occupied habitat patches by the number of all suitable habitat patches. Patches where no host plants were found are considered unsuitable for the Apollo.

	Patches with temperature loggers	All patches censused in 2020
Total number of patches	35	182
Number of occupied patches	14	73
Naïve occupancy	0,42 (n = 33)	0,45 (n = 164)
Total number of larvae	35	257
Larvae n mean	1	1,41
Larvae n of max	5	28
Host plant n mean	183,6	117,72
Host plant n max	1003	1500
Host plant n min	2	1

If comparing the occupancy of the patches investigated for this study, to the occupancy of the patches of the whole census I carried out in the spring and summer 2020, there's not major differences. In the whole census number of patches was 182 (n = 182) and number of occupied patches was 73. Thus, the naïve occupancy is 0,45 (n = 164). Furthermore, the mean number of larvae per patch was 1,41 and maximum number 28. Over ten larvae (n = 12, n = 28) were found only on two patches, and five or more on 19 outcrops. If inspecting the descriptive numbers of host plants, the maximum number of per patch was 1500 stems and the average number 117,72 stems on an outcrop. Host plant densities haven't been counted for the whole census data. (Table 2)

For calculating the host plant densities of censused outcrops, their sizes were computed. When analyzing the data, I realized that there's large differences in the sizes of occupied and not occupied habitat patches (Table 3). Thus, I decided to include the size of habitat patches in the further analysis.

Table 3. Descriptives of size (ha) of occupied (n = 14) and unoccupied (n =21) habitat patches. Occupied and unoccupied patches differ significantly in size (t = 2,364, df = 33, p = 0,012).

	Occupied (n = 14)	Unoccupied (n = 21)
Average size (ha)	3,05	1,42
Median (ha)	3,09	0,64
SD (ha)	1,67	2,19
Max (ha)	6,12	9,28
Min (ha)	0,38	0,02

3.1.2.   Microclimatic temperature on the surveyed habitat patches

Temperatures were collected for a long period of a time on a 0,5-hour interval. The total number of recordings by single temperature logger varied from 5077 up to 6999, depending on the deployment and dissembling date.

Since the study hypothesizes that the habitat patches occupied by Apollo are warmer and more sunbaked, I decided to use separate temperature datasets from spring and summer for the further analysis. This was done to examine if the conditions during the larvae period in the spring, or during the wing-time in the July-August, have an effect to the habitat occupancy of *P. apollo*. Spring data consists of recordings between 29th of May and 15th of June, which is more or less the period when the larvae were found during the census. Whereas, to investigate the temperature differences during the wing-time, I used data from 1st of July and 10th of August. Typically, the wing time of *P. apollo* takes place within this period in Finland (Marttila et al. 1991; Silvonen et al. 2014).

When inspecting the whole dataset (all recordings) of the spring period the mean temperature was 11,94°C, maximum 36°C and minimum -5,5 degrees. The beginning of spring was cold, and temperature rose first time over 20 degrees May 20th. After this, the daily maximum temperatures were ±20°C until the mid-June. The mean temperature of all recordings of the summer period was 17,75°C, maximum 37°C and minimum temperature 4 degrees. (Table 4)

Table 4. Mean, standard deviation, minimum and maximum for spring and summer temperatures, host plant count and density, patch size and patch direction for all studied patches (n = 35). Spring refers to time the period 29.4.-15.6.2020 and summer to the period 1.7.-10.8.2020.

Variable	N	Mean	SD	Min	Max
Spring mean °C	35	11,94	0,42	11,01	12,73
Summer mean °C	35	17,75	0,39	16,98	18,47
Spring max °C	35	32,20	1,78	29,75	36,00
Summer max °C	35	32,52	1,68	30,25	37,00
Spring min °C	35	-3,16	0,85	-5,50	-1,50
Summer min °C	35	6,98	1,09	4,00	8,75
Host plant n	35	183,57	215,98	0	1003
Patch size ha	35	2,07	2,13	0,02	9,28
Host plant dens. (stems/ha)	35	225,56	519,97	0	2750,0
Patch direction °	35	205,2	41,5	110	325

In order to see if there's pairwise correlation between temperature variables or other used explanatory variables, I carried out a Pearson correlation matrix to see if any of the recorded variables have pairwise correlation ($> 0,7$) with another (Table 5). The matrix shows that the only variables with significant correlation are the mean and minimum temperatures of spring and summer. This implies that both of them can't be included when carrying out further analysis. Surprisingly the patch size didn't correlate with any of the temperature variables. (Table 5)

Table 5. Pearson correlation matrix for all recorded explanatory variables. Only the spring and summer mean and minimum temperatures are pairwise correlated ($> 0,7$, bolded) (n = 35).

Variables	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. Spring mean °C	1									
2. Summer mean °C	**0,887***	1								
3. Spring max °C	0,266	0,245	1							
4. Summer max °C	0,132	0,154	0,367	1						
5. Spring min °C	0,449*	0,157	-0,062	-0,157	1					
6. Summer min °C	0,551*	0,232	0,064	0,002	**0,738***	1				
7. Host plant n	0,325	0,401	0,038	0,134	0,073	-0,009	1			
8. Patch size ha	0,348	0,195	0,243	-0,002	0,524*	0,490*	0,278	1		
9. Sedum density (stems/ha)	-0,073	0,149	-0,097	-0,024	-0,543*	-0,588*	0,293	-0,264	1	
10. Patch direction °	-0,145	-0,071	0,089	0,075	-0,267	0,032	-0,195	-0,234	-0,229	1

* $p < 0,01$

When comparing the mean temperatures of occupied and unoccupied patches separately one can see clear difference. In the spring period, the mean temperature of occupied patches was 12,18°C (n = 14, SD = 0,34), whereas the mean temperature of unoccupied patches was only 11,79°C (n = 21, SD = 0,39) (Table 6, Figure 12). In the summer, the mean temperature of occupied patches was 17,92°C (SD = 0,38), and the mean temperature on the patches where the larvae were not found was 17,63 °C (SD = 0,35). (Table 6, Figure 13) Also, for the maximum and minimum temperatures on the occupied patches were warmer than on the unoccupied, except in the spring, when surprisingly the maximum temperatures were higher on the unoccupied ones. Yet, the mean difference was only -0,15476 °C (Table 7). Also, in the summer maximum temperatures the occupied patches are only slightly higher than the unoccupied ones. (Table 6) This could be explained with the effect of increased shading. In the spring the unoccupied patches had less shading, but after foliation the shading increased, which resulted the decreased maximum temperatures in comparison to the occupied ones.

Table 6. Mean average, maximum and minimum temperatures of occupied and unoccupied habitat patches, both in the spring and summer period.

	Occupancy 1/0	N	Mean	SD	SE
Spring mean °C	0	21	11,79	0,39	0,09
	1	14	12,18	0,34	0,09
Summer mean °C	0	21	17,63	0,35	0,08
	1	14	17,92	0,38	0,10
Spring max °C	0	21	32,26	1,83	0,40
	1	14	31,11	1,76	0,47
Summer max °C	0	21	32,46	1,60	0,35
	1	14	32,61	1,86	0,50
Spring min °C	0	21	-3,44	0,81	0,18
	1	14	-2,75	0,75	0,20
Summer min °C	0	21	6,57	1,12	0,24
	1	14	7,59	0,72	0,19

I tested the hypothesis, if the habitat patches occupied by Apollo are warmer than the unoccupied, by comparing the temperature means of unoccupied and occupied habitat patches with independent samples t-test. Analysis was performed separately for spring and summer period, and for means of average, maximum and minimum temperatures. For all

tested variables equal variances were assumed based on the Levene's test (p > 0,05) (Table 7).

The test shows that the occupied habitat patches are warmer than the unoccupied ones, based on mean temperatures of both spring and summer period (Table 7, Figure 12, Figure 13) In the spring the mean temperature of occupied patches was 0,398°C higher than the mean temperature of unoccupied habitat patches, whereas in the summer the average temperature was 0,290°C higher in the occupied patches. Also, the comparison of minimum temperatures supports the hypothesis. In the spring the minimum temperatures of occupied patches are 0,69°C warmer on average than the unoccupied ones, and 1,02 degrees warmer in the summer (Table 6, Table 7, Figure 14). In the spring mean (p = 0,004) and summer minimum temperatures (p = 0,005), the differences were the most significant. However, in the maximum temperatures no significant difference was found, and in the spring unoccupied patches were even slightly warmer than the occupied ones.

Table 7. Results of the independent samples t-test which was used to test the equality of means between occupied and unoccupied habitat patches. Table shows the temperature variables (mean, maximum and minimum) I used to compare the temperature differences of habitat patches. The spring refers to the time period of 29.4.-15.6.2020 and summer to the period of 1.7.-10.8.2020. Minus values in the mean difference column signify that the temperatures of unoccupied patches were higher. The bolded p-values (P) indicate the significant differences (p < 0,05).

| | Levene's Test for Equality of Variances | | t-test for Equality of Means | | | | | 95% Confidence Interval of the Difference | |
	F	Sig.	t	df	P	Mean Difference	Std. Error Difference	Lower	Upper
Spring mean °C	0,328	0,570	3,102	33	**0,004**	0,39762	0,12816	0,13687	0,65837
Summer mean °C	0,145	0,706	2,320	33	**0,027**	0,29016	0,12508	0,03570	0,54463
Spring max °C	0,345	0,561	-0,249	33	0,805	-0,15476	0,62136	-1,41893	1,10941
Summer max °C	0,309	0,582	0,242	33	0,810	0,14286	0,58926	-1,05599	1,34171
Spring min °C	0,044	0,836	2,540	33	**0,016**	0,69048	0,27187	0,13736	1,24359
Summer min °C	3,598	0,067	3,015	33	**0,005**	1,01786	0,33760	0,33100	1,70471

Figure 12. Mean temperatures, ± SE, during the spring period (29.4.-15.6.) of occupied (n=14) and unoccupied rocky outcrops (n=21) by the *P. apollo*. The occupied habitat patches are warmer than the unoccupied ones (Table 7).
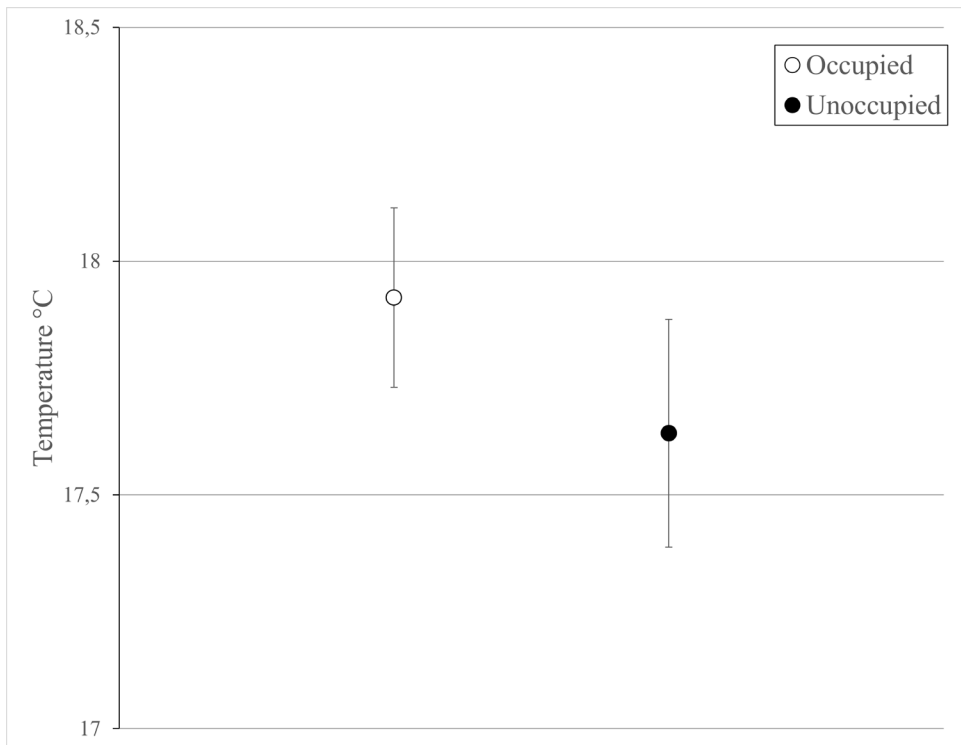
Figure 13. Mean temperatures, ± SE, during the wing-time (1.7.-15.8.) of occupied (n=14) and unoccupied (n=21) rocky outcrops by the *P. apollo*. The occupied habitat patches are warmer than the unoccupied ones (Table 7).
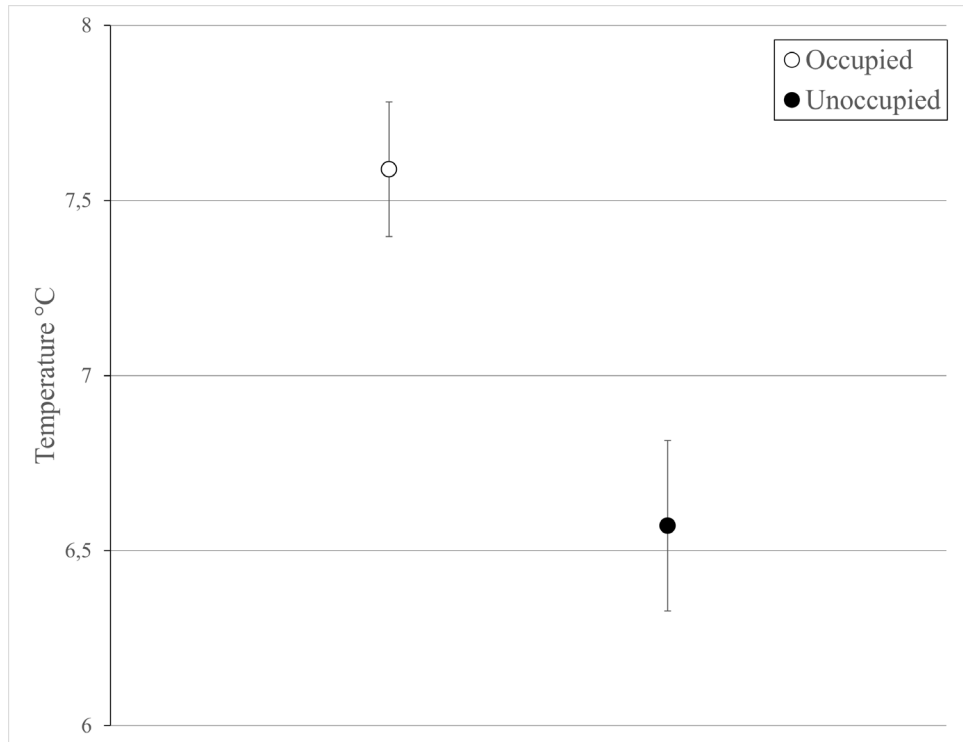
Figure 6. Mean minimum temperatures, ± SE, of occupied and unoccupied patches during the wing-time (1.7.-10.8.2020). Occupied patches are warmer than the unoccupied ones (Table 7).

In addition to temperature variables, I wanted to see if there's significant differences between occupied and unoccupied patches in the number and density of host plants, or in the patch size. When comparing the means, it shows that there's no significant difference in the number of host plants ($t_{33} = 1,465$ p = 0,152) or in the density ($t_{33} = -0,910$ p = 0,185), between occupied and unoccupied patches. Yet, the standard deviation is high and hence the few not occupied patches with high number of host plants may affect the results. When comparing the sizes of occupied and unoccupied patches, I found out that there's significant difference ($t_{33} = 2,364$ p = 0,012) (Table 3).

3.1.3. Effects of different microclimatic temperature variables on occupancy of *P. apollo*

I decided to contrast the effects of different temperature variables with generalized linear model (GLM). The used fixed factors contained all temperature variables (mean, min, max) both for spring and summer and their different combinations (Table 8). However, the

temperature variables that showed pairwise correlation (Table 5) weren't included in the same model. In later stage, I also tested if the models including other recorded explanatory variables, such as patch size, number of the host plants and patch direction would better explain the occupancy data (Table 5).

First, I ran the models by using occupancy (presence/absence) as a response variable and using binary distribution with logit link function. In later stage, I also ran the models by using the number of larvae as a response variable, to see if there's differences in the results (Table 9). To test the model fit for abundance, I ran the models by using both, Poisson and negative binomial distribution with log link function. Negative binomial distribution showed better fit for the model. When using the Poisson distribution, the results showed high risk of overdispersion (Pearson Chi-Square / DF values 1,15-1,86).

After running the different models, I evaluated the model fit based on AIC_c values. The model with the lowest AIC_c value is the most parsimonious model explaining the observations. Furthermore, the risk of over-dispersion was inspected based on Chi-Square / DF value. (Table 8). Due to limited number of observations, I decided not to include the interactions of variables to models.

The AIC_c values of ten top models varied from 42,01 to 48,14 (Table 8). The model 1, including summer mean and minimum temperatures indicated the best fit. It's noticeable that all top three models included the summer minimum temperature (Table 8). Yet, this isn't surprising, since the occupied and unoccupied patches had a clear difference (p < 0,005) when inspecting the minimum summer temperatures (Table 7). Based on the models, all temperature variables have a positive effect on larvae occupancy (Table 8), i. e. warmer temperature (mean, max or min) on a habitat patch, increases the probability of patch being occupied by *P. apollo*. After using only, the temperature variables as explanatory variables in the tested models, I decided to test if including other recorded explanatory variables (e.g. patch size and host plant n) would result a better model fit. Again, the model including both summer mean and minimum temperature, and in addition the patch direction, resulted the lowest AIC_c value (AIC_c = 42,19, Pearson Chi-Square / DF = 0,92). Yet, only the summer minimum temperatures showed significant effect (p = 0,0339), and the direction had an negative effect (estimate = -0,01838). When adding other

than temperature variables, the second-best model included summer minimum temperature and the direction (AIC$_c$ 42,5, summer min p = 0,0196).

Based on the model evaluation, the most parsimonious model for occupancy is the model 1, including summer minimum and summer mean temperatures (Table 8). Yet, since only the summer minimum temperatures have a significant effect (Table 9), it could be interpreted that the model 2 (Table 8), including just the summer minimum temperatures (AIC$_c$ = 42,23) could also well fit the data. Either way, based on the model evaluation and results (Table 8, Table 9), the summer minimum temperature seems to be the most significant temperature variable explaining the larvae occupancy. Parameter estimates and results of type III tests for fixed effects of these two top ranked models are presented in the Table 9.

Table 8. Ten best fit models for occupancy (general linear model, binomial distribution) when testing the model by using only temperature variables (all possible + combinations). Model fit evaluation was based on the AIC$_c$ values (underlined), due to the small sample size (n = 35). The model dispersion was inspected by using Pearson Chi-Square / DF values. In the top models, the number of temperature variables varied from one to three. The direction (positive/negative) of each variables' effect is denoted with +/-, and the asterisk next to the symbol indicates if the effect is significant (p < 0,05).

Model	Spring mean	Spring min	Spring max	Summer mean	Summer min	Summer max	AICc	AIC	Pearson Chi-Square / DF
1				+	+*		42,01	41,23	0,97
2					+*		42,23	41,86	0,98
3	+				+		42,43	41,66	0,94
4	+*						42,78	42,4	1,05
5	+	+					43,15	42,38	1,03
6		+*		+			43,55	42,78	1,04
7				+	+*	+	44,56	43,22	1,00
8		+*					45,09	44,72	1,00
9				+*			46,3	45,92	1,10
10			+				48,14	47,77	1,07

The table shows the temperature variables included in the tested models.
AICc, Aikaike Information Criterion for small sample size The lower AIC$_c$ value indicates better model fit.
Pearson Chi-Square / DF value should be close to 1, values over 1 increase the risk of over-dispersion.

To contrast the effects of different temperature variables for larvae abundance, I carried out similar model evaluation as for the larvae occupancy. I decided to do so, since at least in theory, this could tell if the temperatures could have an effect either on the number of eggs female butterflies have laid to a patch, or on the egg/larvae survival. On the other hand, the number of larvae can be also simply linked to size of the habitat patch. The larger the patch, the more larvae.

As a difference to occupancy models, for larvae abundance I included also the other recorded variables at the first stage. For the larvae abundance the AIC$_c$ values ranged from 89,17 to 101,80. (Table 10). The results are highly similar than for the occupancy, e.g. all temperature variables have a positive effect on larvae abundance. However, the top two ranked models model 1 and 2 (Table 9) also included the patch direction, in addition to temperature variables. Yet, the effect of the direction isn't significant, and thus it could be argued to be irrelevant. The model testing for larvae abundance highlights the effect of summer minimum temperature since it's the only variable with significant effect in all five top models (Table 10).

Table 9. Parameter estimates and type III tests of fixed effects of two top models (Table 8) for occupancy. In both models the effect of summer minimum temperature is significant (p < 0,05, bolded).

Model 1	Parameter est.		Type III tests of fixed effects			
Effect	**Estimate**	**SE**	**Num DF**	**Den DF**	**F Value**	**p**
Summer min temp.	1,1169	0,5214	1	32	4,59	**0,0399**
Summer mean temp.	1,8323	1,1873	1	32	2,38	0,1326
Intercept	-40,9633	21,0817				

Model 2	Parameter est.		Type III tests of fixed effects			
Effect	**Estimate**	**SE**	**Num DF**	**Den DF**	**F Value**	**p**
Summer min temp.	1,3092	0,5372	1	33	5,94	**0,0204**
Intercept	-9,7725	3,9397				

Table 10. Table shows the five top models for the number of larvae (GLM model, negbin distribution), when testing the model with all recorded explanatory variables. Model fit evaluation was based on the AICc values (underlined), due to the small sample size (n = 35). Dispersion was inspected by using Pearson Chi-Square / DF values. Number of variables varied from one to three. In the table, the direction (positive/negative) of each variables' effect is denoted with +/-, and the asterisk next to the symbol indicates if the effect is significant (p < 0,05).

Model	Summer mean	Summer min	Host plant n	Patch direction	AICc	AIC	Pearson Chi-Square / DF
1	+	+*		-	89,17	87,1	0,86
2		+*		-	89,22	87,89	1,00
3	+	+*			89,63	88,3	1,00
4		+*			89,64	88,86	1,06
5	+	+*	+		90,86	88,79	0,97

The table shows the variables included in the tested models. The smaller AIC$_c$ value indicates better model fit. Pearson Chi-Square should be close to 1, values over 1 increase the risk of over-dispersion.

Based on the model evaluation and model results, the summer minimum temperature has the most significant effect on the occupancy of *P. apollo* among the variables I collected for my study. This is supported by the fact, that also for the larvae abundance the summer minimum temperature was included in all five top models, had a positive effect, and was the only variable with the significant effect (Table 10).

3.2. Impact of small-scale thermal variation on the larvae occurrence

In order to investigate the impact of small-scale thermal variation on small-scale larvae distribution within habitat patch (aim 2) temperatures were recorded from three habitat patches (M1, M2, M3) with six temperature loggers on each. (Chapter 2.3.2) Since the temperature was the only collected variable, in addition to the larvae occupancy and larvae exact positioning on the habitat patch, the results concentrate only on comparing the differences of temperatures in patch level.

For aim 1, period from 1st of July until 10th of August was used to investigate the impact of temperatures to the occupancy during the wing time and moreover its effect to the selection of ovipositing sites. Therefore, I decided to use this same period when presenting and analyzing the temperature data collected for the aim 2. The whole dataset consisted of recordings from 12th of June until 29th of August.

When looking at the mean and maximum temperatures of all three patches no clear differences can be seen. Mean temperature varied from 17,83°C (M3) to 17,39 degrees in patch M2. Maximum temperatures varied from 35,75°C to 34,50°C. However, one can see differences between monitored patches when looking at the minimum temperatures. In M3 the lowest measured temperature was 5,75°C, in M2 6,25°C, whereas in M1 it was 7,75°C. (Table 14) Difference of two degrees can be kept notable, especially when the patches are situated in same area. However, as described previously (Chapter 2.3.2), the type and characteristics (slope, shading, openness) of all three patches slightly vary, and this may explain the differences in minimum temperatures.

Table 11. Mean, maximum and minimum temperatures (1.7.-10.8.2020) and number of observed larvae for the three investigated habitat patches.

	M1	M2	M3
Mean °C	17,68	17,39	17,83
Max °C	35,75	35,50	34,50
Min °C	7,75	6,25	5,75
Larvae n	3	1	2

When inspecting temperatures on a patch level, by comparing the temperatures of cells that had small larvae, to the temperatures of cells with only host plants, one can see more clear differences. For all patches, the measured mean, maximum and minimum temperatures are higher in the cells that included larvae, except on the patch M3, where the mean and maximum temperatures were higher in the cells that had no larvae (Table 15). Furthermore, when comparing the recordings of all patches together, the mean, maximum and minimum temperatures are higher in the cells that included both the larvae and host plants.
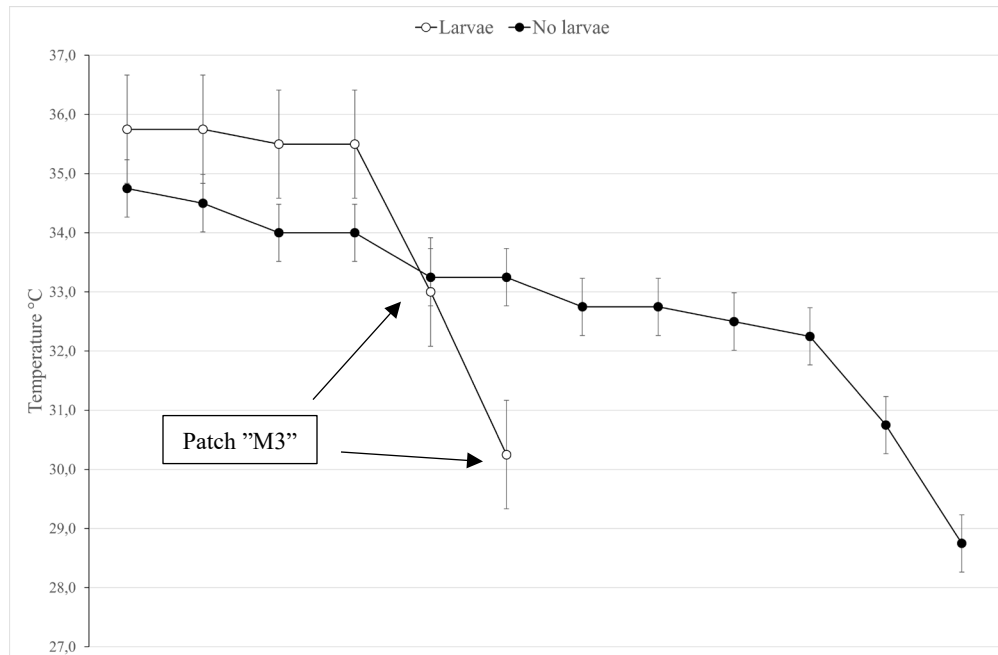
Figure 7. Maximum temperatures, ± SE, of the cells including both larvae and host plant (n = 6), and the cells with just host plants of all three monitored patches (n = 12). The difference of maximum temperatures had the lowest p-value (p = 0,13) when comparing the means of different temperature variables for all patches. The two last dots (pointed with arrows) are the ones that located on the patch M3, where the maximum temperatures were higher in cells with no larvae.

Table 12. Mean temperatures of the period 1.7.-10.8.2020 of the cells where both larvae and host plant were observed (n = 6) and the cells where only host plants were found (n = 12) of all three investigated habitat patches (M1, M2, M3), and mean and max temperatures of all patches presented separately. Only on the patch M3, the mean and maximum temperatures were higher in the cells where no larvae were found. Only when observing the maximum temperatures of the patch M1 the cells with larvae were significantly warmer (bolded, p = 0,02).

	Larvae	**N**	**Mean**	**SD**	**SE**
All Mean °C	no	12	17,56	0,47	0,14
	yes	6	17,79	0,31	0,13
M1 Mean °C	no	3	17,48	0,23	0,13
	yes	3	17,88	0,35	0,20
M2 Mean °C	no	5	17,28	0,53	0,24
	yes	1	17,97 .	.	
M3_Mean	no	4	17,97	0,23	0,12
	yes	2	17,57	0,28	0,20
M1 Max °C	no	3	33,17	0,72	0,42
	yes	3	**35,67**	0,14	0,08
M2_Max	no	5	32,30	2,49	1,11
	yes	1	35,50 .	.	
M3_Max	no	4	33,13	1,01	0,51
	yes	2	31,63	1,94	1,38

I tested the hypothesis, if the small-scale microclimatic temperature variation affects the fine-scale distribution of larvae on a habitat patch by comparing the temperatures of the cells with larvae and host plant, to the temperatures of cells that included only host plants and no small larvae. Similar to above, the comparison was carried out by comparing the means with independent samples t-test. Analysis was performed separately for means of average, maximum and minimum temperatures, both separately to all three patches and to data of all patches combined.

Based on the tests, the cells (locations) with larvae are warmer temperature only when inspecting maximum temperatures of the patch M1 ($t_{2,16}$ = -5,883, p = 0,02). However, relatively low p-values show indication of larvae preferring warmer cells, also when looking at the mean temperatures of the patch M1 (t_4 = 1,679, p = 0,17), minimum temperature of patch M2 (t_4 = 2,24, p = 0,09), and when comparing the maximum (t_{16} =

1,601, p = 0,13) (Figure 17) and minimum (t_{16} = -1,371 p = 0,19) temperatures of all patches together. Furthermore, it needs to be noted that the difference of mean temperatures is also quite low in the patch M3 (t_4 = 1,887, p = 0,13), where the mean temperatures were higher in cells where no larvae were found. For the other tested temperature variables, the p-value varied between 0,26 – 0,73.

Since the number of patches was so low and other variables weren't recorded, I decided not to carry out any further analysis. I discuss and highlight the deficiencies and problems of this part of my study in the chapter 4.2.

4. Discussion

The goal of my study was to investigate if the microclimatic temperature differences and variation effects the occupancy of Apollo butterfly in the Parainen distribution area. To do so, I installed temperature loggers on 35 habitat patches (rocky outcrops) and carried out census of *P. apollo* larvae and their host plants (*H. telephium*) on the same patches (aim 1). Furthermore, I piloted if the small-scale thermal variation within habitat patch has an impact to fine-scale distribution of larvae within habitat patch, which could imply that thermal variation affects either the selection of ovipositing locations of female butterflies or the larval survival (aim 2).

4.1. Microclimatic temperature variation and the occupancy of the Apollo butterfly

To answer the question, I compared the temperatures of occupied and unoccupied patches, and modelled the effects of different variables on occupancy and larvae abundance by using generalized linear model. The results showed that patches with warmer microclimate are more likely to be occupied than the cooler ones, when comparing mean and minimum temperatures. The comparison was made separately for spring (larvae period) and summer (wing-time), and the differences were significant for mean and minimum temperatures. Only in the maximum temperatures significant differences weren't found. This is most

likely since all selected habitat patches were relatively open and similarly warmed by the sun at some time of the day. Thus, the maximum temperature isn't as relevant for the habitat suitability, as the mean and minimum temperature. However, it may be a significant factor in smaller scale through thermoregulation and microhabitat use of larvae and ovipositing behavior (Ashton et al. 2009; Curtis & Isaac 2015). Both when simply comparing the temperatures, and contrasting the effects of different temperature variables by using GLM, the effect of temperatures during the wing-time (i.e. summer), and especially the minimum temperature was highlighted (Table 8, Table 10). Also, the mean temperature in larvae period (i.e. spring) seems to have a role on larvae occupancy (Table 8). Furthermore, models including patch direction (degrees) resulted low AIC$_c$ values. Patch direction showed negative effect, i.e. patches with main direction more towards southwest/west were more unlikely to be occupied. In theory, like in other studies (Wilson et al. 2014), this could be related to so called false-spring events (Descimon et al. 2005; Schmeller et al. 2011). False-spring events may cause larvae to emerge too early in the springtime when the sudden cooling of weather may increase larvae mortality. Effect is linked to the warming of climate. These false-spring events may play a role for *P. apollo* in Finland, especially since its range is restricted to the areas most affected by warming of winters.

I find the role of minimum temperatures during the wing-time on larvae occupancy highly interesting. When looking at the raw data I noticed that the lowest temperatures often occurred in the early hours just before sunrise, and quickly began to rise after the sun rose. Without further analysis, this seemed to be the case especially in occupied patches. The minimum temperature of a rocky outcrop is most likely affected by its openness, direction, altitude, and wind. Since no interaction between the minimum temperatures and patch size wasn't found, it could be concluded that the openness isn't perhaps a major factor affecting the minimum temperature. Thus, I supposed that the most open patches can be more exposed to the wind and lowering of temperatures in nighttime, than the ones were trees give a shelter. When I further inspected this, I found out that the patch with the highest host plant count (1008 stems) had also the lowest minimum temperature in the summer (4,75°C). Surprisingly, the same patch is the third warmest of all if comparing the minimum temperatures of the spring period. This most likely due to its characteristics. The patch is an open rocky meadow in the middle of low-lying fields which possibly makes its

vulnerable to temperature drops during nighttime in summer and more exposed to the wind. As the occupied patches are also warmer when inspecting the mean temperatures, it could be interpreted that the *P. apollo* might favor patches with more stable temperature conditions. Furthermore, these patches may provide more microclimatic niches within a patch than the most open ones (Ashton et al. 2009). Also, it may be that the female butterflies favor the patches that warm up earlier and hold their temperature better which can be related to groundcover. However, it needs to be noted that the larvae mortality can't be excluded when making the conjecture. Ashton et al. (2009) noticed that larvae preferred microhabitats with barer groundcover and dead vegetation in areas with lower ambient temperature. Furthermore, they found out that these microhabitats are warmer than the ambient air. Thus, also in Parainen, at the northern range margin of *P. apollo*, the occupancy and larvae abundance can be related not only to the warmth of the patch, possibly related to openness, but only with the groundcover.

As mentioned, the occupied patches were also larger than the unoccupied. Therefore, the results can't totally exclude the chance that the larger, and better connected, habitat patches could explain the occupancy (Hanski 1998). Especially, when the most occupied patches were located within same area in Lemlahdensaari island. Larger patches may form a working and viable patchy population (Brommer & Fred 1999), whereas e.g. on the Stortervolandet island the isolation and weakening of habitat suitability may have resulted the decline of local population in the past twenty years. Nevertheless, my results show that the temperature may be a key factor for habitat suitability of *P. apollo*. This is supported by the fact that the habitat patches within the former *P. apollo* stronghold in the Stortervolandet island (Brommer & Fred 1999), are suffering from overgrowth, which most likely have resulted in lowering of temperatures, but hasn't significantly affected the number of host plants. Apart from favoring the warmer conditions, the female *P. apollos* may prefer larger patches since they are more likely to provide more thermal variation (temperature niches), and hence more options to select the ovipositing location. (Curtis & Isaac 2015) Of course, when making this conclusion, I assume that the temperature has an impact on the selection of the ovipositing locations. Apart from the thing discussed above, the size may also explain why the occupied patches are warmer based on mean and minimum temperatures. Furthermore, the study design and actual deployment of temperature loggers, may explain why there's not major differences in maximum

temperatures. All temperature loggers were similarly deployed on the most open area of each outcrop, and most patches are directed to the midday sun (Figure 9). Differences in the patch size however, and the amount of shading (openness) related to it, may explain the larger deviation in maximum temperatures.

Finally, I want to highlight one disadvantage of my study design that I figured out early stage when carrying out the field work. The used definition of habitat patch resulted large variation in size. Furthermore, the large size of a patch caused situations where the distance of found larvae and temperature logger was long. Yet, in some cases the distance between larvae and logger was only few centimeters. Nevertheless, this may have biased the results since the microclimatic temperature may differ significantly between locations. If I would carry out the study again, I would rather deploy multiple temperature loggers within a single patch, (e.g., n depending on size). This would enable to not only to compare the temperatures of habitat patches in relation to occupancy, but also to see how the thermal variation affects the habitat use and occupancy within a patch. Furthermore, this could reveal if annual fluctuations in ambient temperature, together with the availability of microclimatic niches, have an impact to the occupancy and abundance and furthermore to ovipositing behavior, as it has for the Glanville fritillary (e.g. Ashton et al. 2009; Curtis & Isaac 2015) Moreover, the use of other temperature variables derived from the data, e.g. daily mean temperature or the temperature sum, could reveal and provide new information and insights.

4.2. Effects of small-scale thermal variation in the habitat patches

The results of my study show that fine-scale microclimatic temperature variation within rocky outcrops does occur. It even may have an impact on the ovipositing locations or larvae survival of *P.* apollo in the studied population, yet this isn't evident due to shortages of my study and ambiguous results.

However, when looking at the results, it is interesting that when investigating microclimatic temperature variation in micro-scale on a habitat patch level, the maximum temperatures show large differences (also variation) between occupied and unoccupied cells. Also, the maximum temperature is the only factor where the significant temperature difference was

found (only on one patch). Yet, it needs to be noted that the results are also controversial. For one investigated patch, the temperatures are higher in places where no larvae were found. Nevertheless, this is interesting compared to the results of aim 1, where occupied and unoccupied patches showed no difference in maximum temperatures.

When investigating the ovipositing behavior of the Glanville fritillary, Curtis et al. (2015) found out that the female butterflies favor plants that are warmer than the temperature of surroundings. They concluded that females oviposit on warmer host plants since warmer conditions benefit the larvae growth and development. The connection of temperature and butterfly larval development has been acknowledged also in other studies. (Renwick & Chew 1994; Doak et al. 2006). Furthermore, this behavior may be pronounced in populations living in higher latitudes or altitudes near their distribution edge (Thomas 1991; Merrill et al. 2008), such as *P. apollo* in Finland. When the environmental conditions affect the habitat availability and suitability, and hence limit the distribution, it is intelligible that females to try to maximize the larvae survival and development by using time and effort in the selection of ovipositing location. When considering my results and the findings made in some other studies (e.g. Ashton et al. 2009; Curtis & Isaac 2015), I think that temperature may play a role either in the selection of ovipositing locations or larval survival or microhabitat selection of *P. apollo*. Fred & Brommer (2003) showed that, at least in the outer archipelago population, female Apollos' lay their eggs off the host plants, yet the ovipositing isn't totally random. Could it be that the female butterflies lay their eggs on microclimatic niches which they found favorable for larvae survival and development? This is supported by the fact that both behavior and micro-habitat selection of *P. apollo* larvae seem to be affected by the ambient temperature and microclimatic temperature variation (Ashton et al. 2009; Wilson et al. 2014). Also, microclimatic temperature variation affects to ovipositing of other butterfly species (e.g. Eilers et al. 2013; Curtis & Isaac 2015), and furthermore the ovipositing behavior and abundance may be also affected by the annual variation of ambient temperature (e.g. Curtis & Isaac 2015). However, it can't be excluded that the selection of detailed ovipositing location of *P. apollo* may be also affected by solar radiation (sunlight), which of course is most likely more or less linked with the temperature. When studying the role of olfaction and vision in location of host plants, Fred & Brommer (2010) found out that small *P. apollo* larvae often headed towards the sun and were unable to locate host plants from distance.

To get more evident proof of temperatures role the similar study should be carried out with larger quantity of observed patches and in more detailed and designed way. More attention should be paid to device setup, study design and the role of other factors. One way could be to measure surface temperatures of specific ovipositing locations (either plants or ground) with handheld thermometer (Ashton et al. 2009; Curtis & Isaac 2015). Of course, this would require visual observation of ovipositing female Apollo butterflies. However, this has been carried out successfully in earlier studies (Fred & Brommer 2003). Moreover, the role of annual variation should be considered, and at the best-case scenario the temperature monitoring would be done for longer period and for multiple years.

One of the aims of this study, was simply to pilot if thermal variation has a role in the selection of ovipositing location or larvae survival of *P. apollo*, and thus encourage further studies. Ashton et al. (2009) have already shown, that at least for population of *P. apollo* living in high elevation, ambient temperature affects larval microhabitat selection of and habitat use, and small-scale habitat variation is important for thermoregulation of larvae. It's clear that in further studies, more attention should be given to the design of the study, collection of additional variables (e.g. groundcover) and detailed census and observation of ovipositing behavior. Together with temperature monitoring, the visual observations of females laying their eggs and/or novel monitoring methods of larvae behavior (Dolek & Georgi 2017), could reveal new information on the ovipositing behavior of Apollo butterfly, which could be important when planning and implementing conservation and habitat restoration measures (Fred & Brommer 2003).

4.3. Main conclusions and future research

The results of my study show that based on larvae census, the microclimatic temperatures are related with the habitat occupancy of *P. apollo*. In the other words, larvae were found from outcrops that were warmer than the unoccupied ones (Table 6, Table 7). Furthermore, the warmth seems to affect the abundance of larvae (Table 10). Especially, higher minimum temperatures on a habitat patch, during the wing-time in June-August, seem to have important role on occupancy, presumably through temperature stability. Apart from populations living in other regions, this may be pronounced in northern range, due to

changeable weather conditions in the summertime. Therefore, it's reasoned to say that temperature may be an important factor of habitat quality for *P. apollo*. However, environmental variables, such as temperature, could play a role not only for occupancy or abundance of *P. apollo*, but also for the survival of small newly hatched larvae or wintering eggs. This possibility can't be excluded based on my study. Furthermore, annual variation in ambient temperatures and precipitation may also affect the amount of suitable nectar resources. Fred & Brommer (2009) showed that in the archipelago population the female Apollo butterflies are prone to emigrate from the island to another in a search of nectar plants. This may cause the patch to be abandoned if migration back to the island doesn't occur.

 Nevertheless, the results can be considered valuable for the purposes of site management. As temperatures are mostly affected by the sunlight, the study shows that even small-scaled clearing could make a difference when restoring habitats of the Apollo butterfly. Furthermore, the persistence of *P. apollo* may be dependable on the amount of suitable and available habitat patches, and their connectivity (Brommer & Fred 1999; Fred et al. 2006). On forested habitat patches, even the increased shading of single trees may cause them to change unsuitable in time if the host plants are shaded. As the Apollo restricted to sole host plant, the meaning of this is highlighted in the most sunbaked habitat patches were often the densest growths of orpine plants are situated in the lower slopes of rocky outcrop (personal observation). Furthermore, the preservation of microclimatic thermal variation, through microhabitats, needs to be considered in restoration measures, since it will buffer the annual variations in weather that are increasing due to climate change (e.g. Roy & Thomas 2003; Oliver et al. 2012; Curtis & Isaac 2015), and is proven to be important for factor for microhabitat use and thermoregulation of *P. apollo* (Ashton et al. 2009).

Recent studies (Kukkonen 2021, Kukkonen et al. 2022) show that the decline of Apollo butterfly can't only be explained with the occurrence or density of the host plant, even though earlier studies have concluded that the density of host plant is the most significant factor explaining the habitat occupancy of *P. apollo* (Brommer & Fred 1999; Fred & Brommer 2010, 2003). As a distinction to my study, the studies (Kukkonen 2021, Kukkonen et al. 2022) are carried out in the outer archipelago, where the *P. apollo* mainly inhabits small treeless barren islands close to the open sea. Hence, both the ambient temperature and microclimatic conditions and their variation most likely differ significantly

from my study area. However, in those open habitats the thermal niches and variation, created by sheltering terrain (e.g. cliffs and rocks), vegetation shrubs (e.g. juniper and heather) and amount of bare ground, may play even more important role, since the temperature conditions are generally lower and more varying during the larvae period than in the coastal area (Ashton et al. 2009). Furthermore, in the outer archipelago the increased fluctuations in weather caused by climate change are clearly visible. Warming climate has caused major changes in the ice coverage of the Baltic Sea and more often the winters are snowless. (Ilmatieteen laitos 2023) Moreover, the temperatures often range close to 0 degrees, causing constant variation between snowmelt and freezing. Due to climate change the mean temperature is predicted to rise in the southwest Finland in future, but at the same time precipitation will increase and snow coverage and the number of frosty days will decrease. Also, the wind speeds predictably will rise and this most likely will affect the most to microclimatic conditions of the outer archipelago. (Ilmasto-opas 2023) Consequently, the role of both microclimatic variation and changes in ambient temperature and other climatic conditions may have a role explaining the decline of *P. apollo* in Finland, and hence the climate change and stochastic weather events may threaten the existence of the Apollo here on its northern range edge in future. This is eminently important, as the species is restricted to single host plant, occurring only in the southern part of the country which climate will be highly affected by climate change.

In conclusion, a more knowledge should be gathered on the role of microclimatic thermal variation, habitat heterogeneity and annual temperature to the occupancy of the *P. apollo*. This may reveal new and essential information of the factors affecting the distribution and abundance of the Apollo butterfly in Finland. In order to prevent the local extinction of this beautiful butterfly we need targeted and urgent conservation measures.

5. Acknowledgements

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