Ability to adjust breeding time to earliness of spring

- a comparative study of four passerine bird species

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Abstract

During the last century, the average global temperature has increased significantly and many species have responded to this increase by advancing the time of reproduction. Climate change has advanced the laying date in many bird species across Europe, although this varies between populations within the same species and between different species. The main selection pressure for birds to advance their laying date is to match the shifting phenology of species in the underlying trophic levels. Birds adjust their laying time so that the offspring will be raised when food is most plentiful.

In this thesis, I have studied how four passerine bird species, namely the nuthatch *Sitta europaea*, blue tit *Cyanistes caeruleus*, great tit *Parus major* and pied flycatcher *Ficedula hypoleuca*, in a woodland study area with nest boxes, at Dæli, S. Norway, have adjusted breeding time in response to spring temperature (2003-2016). The annual mean spring temperature, precipitation and snow depth have not increased significantly in the study area during this period. This is in concurrence with that annual mean laying date has neither advanced for any of the four species. Nevertheless, there has been a strong correlation between annual spring warmth sum and annual laying date for the nuthatch, the blue tit and the great tit. In years with high spring temperature, birds advanced their laying date and respectively laid later when temperatures were low. The nuthatch additionally delayed its laying date by approximately two days per 100m increase in altitude. The pied flycatcher laying date was weakly correlated to early spring temperatures due to it being a long-distance migrant and not arriving at the breeding grounds until early May. The most important 20-day pre-laying temperature period, that gave best support to the observed mean laying date, was significantly correlated to the mean laying date for each individual species. The mean laying date for the four species was 20 April for the nuthatch, 1 May for the blue tit, 3 May for the great tit and 23 May for the pied flycatcher. For all of the species, the mean laying date occurred ~10 days after the end of their most important pre-laying temperature period.

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1 INTRODUCTION

Timing of reproduction is among the most important life-history decisions an organism has to make and it has an impact of the individual's fitness (Visser et al. 2009). For many species, there is a short period during the year where the conditions are favourable for breeding. This period varies from year to year, due to fluctuations in the environment. Nearly all phenological phases correlate with spring temperature and spring temperature is the main climatic factor controlling spring phenology (Walther et al. 2002). Annual variations in phenology has also been linked to the North Atlantic Oscillation (NAO from here on) (Forchhammer et al.1998; Sanz 2002, 2003; Stenseth et al. 2002). The NAO determines most interannual fluctuations in the winter temperatures, where high positive NAO-index leads to high winter and spring temperatures and vice versa (Hurrel 1995). The North-Western Europe is especially affected by the variation in the NAO (Sanz 2003; Ottersen et al. 2001; Hurrel 1995). The NAO does not work directly on the birds per se, but rather on the phenology of their prey (Sanz 2003).

Since the 1960s, many spring phenomena are occurring earlier such as flowering of plants, endings of hibernation in mammals, and migration and breeding in birds (Walther et al. 2002). Many publications have reported various responses to climate change by advancing their phenology (Parmesan & Yohe 2003; Matthysen et al. 2011; Walther et al. 2002; Dunn 2004). Parmesan and Yohe (2003) did a meta-analysis of 677 species from different taxonomic groups and found that 62% showed a trend towards earlier phenology, which is in accordance to the warming temperature (IPCC 2013). Although most species are advancing their phenology, there are also organisms with no response (Parmesan & Yohe 2003; Both et al. 2004; Crick & Sparks 1999) and species who delay their phenology (Parmesan & Yohe 2003). Understanding the mechanisms and decisions of which birds adapt to a changing climate is crucial both for short- and long-term consequences. I will present some of the challenges and constraints that influence the life-history of some passerine birds species. There is a vast amount of research on the blue tit *Cyanistes caeruleus*, the great tit *Parus* major and the pied flycatcher *Ficedula hypoleuca* in relation to phenology and climate change. The nuthatch *Sitta europaea* however, is less studied with most of the studies being related to foraging and nesting behaviour. I will focus on findings from Europe, although some of the same results are present in North American bird species as well (see Brown et al. 1999; Dunn & Winkler 1999).

1.1 Climate

During the last century, the average global temperature has increased significantly. According to the Intergovernmental Panel on Climate Change (IPCC 2013), the globally average temperature has increased by 0.85 (0.65 to 1.06) °C. The periods 1910-1945 and from 1976 and onwards are those most responsible for the increased warming (Walther et al. 2002). Especially the last three decades have been successively warmer than any other decades recorded, with the 2000s being the warmest (Hartmann et al. 2013). Effects of climate change on birds is mostly noticeable in studies on the time of breeding and the synchronization of peak food abundance. In years with warmer temperatures, birds start egg-laying earlier in approximately 60% of the studies done (Dunn 2004). Nevertheless, it is clear that there are differences in the way to which birds respond to climate change, both between and within species (Matthysen et al. 2011; Sanz 2002). The individuals need to be able to respond and adapt to a changing environment, and they need to do it rapidly and efficiently (Charmantier et al.2008). Phenotypic plasticity provides this, and is occurring in different passerine bird species in Europe. Pigliucci (2001) defines phenotypic plasticity as *“the property of a given genotype to produce different phenotypes in response to distinct environmental conditions”.* Phenotypic plasticity allows an organism to adapt its phenotype to a changing environment. This is of great importance in the synchrony between predators and pray interaction in the tritrophic system (Durant et al. 2007) of passerine bird. The tritrophic system of passerine birds is the feeding on caterpillar prey, which in turn feed upon the emerging leaves (Visser et al.1998; Nussey et al. 2005). The match-mismatch, of these interactions, largely affect the timing of reproduction and growth for the organisms involved (Stenseth et al. 2002), with temperature being the controlling factor.

1.2 Food abundance

Both the blue tit, the great tit and the pied flycatcher rely on caterpillars (e.g. the winter moth *Operophthera brumata*) as the main food source for their nestlings (Slagsvold 1976; Perrins 1965; Perrins & McCleery 1989). Caterpillars are also one of the important food resource for the nuthatch, and its nestling, in addition to spiders and beetles (Matthysen 1998). The caterpillars live on all types of deciduous trees and enters a bud at budburst in early spring to feed on the young leaves (van Dongen et al. 1997). The caterpillars prefer the newly emerged leaves because they contain more nutrients and are less tough than more mature leaves (Feeny 1970). A diet consistent of mature leaves usually leads to lower fitness for the caterpillar (van Dongen et al. 1997). The time when the caterpillar is most abundant and easily available to the birds is termed “half-fall” (van Noordwijk et al. 1995; Perrins 1965). Perrins (1965) defined the “half-fall” as the date at which half of the larvae has fallen from the trees to the ground, where they bury themselves to pupate. Metamorphosis is strongly temperature dependent, as caterpillar growth and pupation proceeds more rapidly during warmer weather conditions (Both & Visser 2005; Smallegange et al. 2010). The caterpillars are therefor only available to the birds during a short period in the spring when the caterpillars are feasting on newly emerged leaves on their host tree (Hinks et al. 2015; Visser et al. 2006). It is therefore important that the birds synchronize their breeding time, so that the peak abundance of caterpillar prey matches the time when food is most needed for their offspring (Lack 1954; Durant et al. 2007; Visser et al. 2006; Smallegange et al. 2010). The period at which food resources are favourable varies from year to year. The peak of caterpillar biomass can vary annually with three weeks, and thereby affecting the birds breeding cycle timing to vary annually (Visser et al. 2006).

Since the caterpillars are the main food source of these insectivorous bird species, as mentioned above, it is important that they adapt to the changes of their environmental phenology to optimize synchronization (Schneider 2008). However, it is often difficult to accomplish this, and the mismatch between food supply and nestling demands have been documented by multiple researches (Visser et al. 1998,2006; Both & Visser 2001; Slagsvold 1976; Dunn et al. 2011; Dunn 2004 and refs therein).

1.3 Limitations to early breeding

It is well known that birds who breed earlier in the season often are more successful than those who breed later (Perrins 1996; Stevenson & Bryant 2000; Perrins 1970). Earlier breeders usually have larger clutch size, larger eggs and produce heavier fledglings (Perrins 1996; Enoksson 1993). There is therefore often a selective advantage by breeding early, so why is not this the generalized trend among the study species? There is a limit to which extent they can advance their laying date. Perrins (1965) suggested that the disadvantage by early breeding is related to the females own fitness. The female needs ample amounts of food both for general body maintenance, and the production of eggs. During low temperatures, the energetic cost of maintenance for small birds is also higher, which in turn has an impact of the female’s fitness (Stevenson & Bryant 2000; Crick 2004). The female has to make a decision using phenological ques such as temperature, to weight the trade-offs of having enough food during egg production and making sure that the offspring hatch at the time of peak food abundance. The females often have to make the decision when to start breeding at a time when food is usually less abundant, due to the time elapsing between the start of ovum growth and the hatching date which takes around 22-26 days (Perrins 1996; Perrins 1970). It takes at least three weeks between the date at which food becomes available for the female and she is able to start the breeding cycle, and the date when there can be young in the nest (Perrins 1970). This might be one of the constraints on why they are not breeding earlier. Looking at female nuthatches, older individuals are more efficient foragers, thereby acquiring food quicker and hence have an earlier laying date than the first-year females (Enoksson 1993). This is an example of how food requirement may influence the laying date of nuthatches.

1.4 Various responses to temperature

Laying date

Crick et al. (1997) found that the laying date for many British bird species (31%) had significantly advanced during 1971-1995, and that many more showed a tendency for earlier laying. McCleery and Perrins (1998) found similar result for the British great tit population in Wytham woods, where there was a significant advancement in laying date from the 1970s, but there had been no such trend in the 24 years period preceding 1970. This shows that the great tits of Wytham woods are able to maintain the synchronization between food requirements for nestlings and food abundance, with the consistently increasing temperature (Stevenson & Bryant 2000). An increase in laying date since the 1970s has also been observed in nuthatch populations in the Czech Republic (Bartošová et al. 2014). This is in agreement to Walther et al. (2002) findings, that most of the global warming has occurred after the 1970s. This shows that there is a clear correlation between advancement in laying date and increasing temperatures.

This is interesting in regard to other studies of great tits and blue tits in other parts of Europe. In a great tit population in Hoge veluwe, Netherlands, the laying date had not advanced during 1973-1995 (Visser et al. 1998). The temperature on the other hand had increased and was correlated to the caterpillar peak abundance (Visser et al. 1998). Visser et al. (2003) found similar results for populations of great tit and blue tit in Finland, France, Russia, United Kingdom (Treswell) and three more populations in the Netherlands. In their meta-analysis of 24 populations of great tits and blue tits, across six European countries, they found that laying date had only advanced in eight out of the 24 populations (Visser et al. 2003; see also Dunn 2004). Populations across the borders, and within each country, had responded differently. The northern populations in Russia and Finland had not advanced laying date, nor had the temperature significantly increased (Visser et al. 2003). However, populations within the same proximity in Belgium and Netherlands, who experienced the same increase in temperature, responded differently (Visser et al. 2003; Dunn 2004). To the variations in laying date, Visser et al. (2003) proposed that the temperature hypothesis might explain the variations among the different great tit and blue tit populations at different locations. The temperature hypothesis states that the increase in spring temperatures occurs at different stages during the breeding cycle at different locations (Visser et al. 2003). The temperature hypothesis could account for the differences observed in the UK populations, where both pre-laying and breeding temperatures had increased. In Belgium and the Netherlands, the temperature had only increased during breeding, the temperature hypothesis could thereby not account for the differences observed in these populations.

Clutches

The occurrence of second clutches was suggested as an explanation for the variation observed between tit populations in Belgium and the Netherlands (Visser et al. 2003). Individuals in double-brooded species should be selected to start breeding earlier, so that the first clutch hatches before optimal conditions are reached leaving time to produce a second smaller clutch (Crick et al.1993). Single-brooded species should lay at the optimal time of peak food abundance and follow the annual shifts (Crick et al. 1993; Dunn 2004). As Visser et al. (2003) predicted, populations who advanced their laying date in accordance to peak food abundance also showed a decline in double-broodedness, similar results were found in other tit populations (e.g. Visser et al. 1998; Matthysen et al. 2011; McCleery & Perrins 1998; Smallegange et al. 2010).

Double-broodedness and replacement clutches are seldom found amongst the nuthatches (Enoksson 1993). The reason for this is thought to be due to it being a territorial species, where fledging date is just as important as laying date (Enoksson 1993). Early fledging date is crucial for the juveniles to be able to secure a vacant high-quality territory to settle in (Matthysen 1989; Enoksson 1993) where "*first come, first served"* applies. Late fledglings will have a hard time finding a territory of any worth, resulting in minimal survival and unnecessary energy expense for the female (Enoksson 1993). Multiple studies have shown that early laying in nuthatches are connected to high spring temperatures (Matthysen 1989; Schmidt et al. 1992; Bartišová et al. 2014), but also the forest type, especially oak-dominated forest, has an influence on early laying in nuthatches (Schmidt et al. 1992).

Incubation

Individuals can also be phenotypically plastic, concerning the onset and timeframe of their breeding. The ability of birds to strategically control the interval between laying date of first egg and hatching date, may reduce the effect of unforeseen changes in the environment resulting in a mismatch with the peak of food abundance (Cresswell & McCleery 2003). The females can alter the laying-hatch date interval in several ways. They can do it by modifying the laying date, clutch size, laying interruptions, onset of incubation and incubation time (Matthysen et al. 2011; Visser et al. 1998; Cresswell & McCleery 2003). The long-distance migratory pied flycatcher has since the 1990s advanced it’s laying date at the breeding ground in the Netherlands, to be able to match the advancement in food peak (Both & Visser 2005). In response to not being able to advance the arrival time at breeding grounds, the pied flycatcher has advanced their laying date by shortening the time elapsed after arrival and egg-laying (Both & Visser 2001). During warmer years, this advancement was not strong enough and to compensate the pied flycatcher started incubation earlier, thereby advancing the hatching date (Both & Visser 2005). This strategy, to reduce the time between clutch completion and incubation, has also been used by the great tit population in Hoge veluwe, Netherlands (Visser et al.1998). These great tits are constrained from advancing their laying date (Visser et al. 1999, 2003; this paper) and by reducing the laying-hatch date interval, they are minimizing the mismatch with peak food abundance.

Trying to match the advancement in peak food abundance, by consistently laying early, may sometimes backfire. Sometimes after egg-laying has started, or even been completed, the weather can suddenly turn and become cold (figure 1). This influences the food peak by being delayed (Cresswell & McCleery 2003), leaving the birds with no nestling food at the time they hatch. An increase in laying interruptions during unfavourable weather is often present in great tits, blue tits, nuthatches and pied flycatches (Schmidt & Hamann 1983; Cresswell & McCleery 2003). For the great tits in Wythan wood, UK, indivuduals with uncompleted clutches ended up with larger clutches and delayed incubation. Nests with no eggs laid yet would postpone until better conditions and then reduce incubation time to match the food peak (Cresswell & McCleery 2003). Nuthatches are also known to delay incubation, and are able to do so by up to 8 days under poor weather conditions (Schmidt & Hamann 1983; Löhrl (1958) in Matthysen 1998). During spring 2013 a period of cold weather struck Dæli study site in Norway, many tits had already started egg-laying and some nests where completed. The tits where not able to compensate by altering the laying-hatch interval sufficiently enough, leading to almost 2/3 of the nests failing (T. Slagsvold pers. com.). This shows that the variation in response among species are extensive (Matthysen et al. 2011; Visser et al. 1998; Cresswell & McCleery 2003).

Figure 1. After three weeks with increasing temperature, bare grounds and budburst occurrence. On 30 April 2016, the weather suddenly changed and temperatures dropped by 2.5°C and snow covered the ground. (© Emilie Mutch).

Complex changes in the temperature patterns are influencing the breeding cycle among birds, in many different ways (Stevenson & Bryant 2000). Being able to adjust and reduce the mismatches is of great importance, and can to a large extent be explained by phenotypic plasticity (Matthysen et al. 2011). Most of the constraints and reposes above have been explained in relation to the timing of egg-laying and the proceeding steps. However, long-distance migratory species experiencing additional constraints and challenges prior to arriving at the breeding ground, in regards to climate change.

1.5 Migration

Both the blue tit and the great tit are known for some short-distance migration among the juveniles (Haftorn 1971), while for the most part the population is resident. The nuthatch does not migrate and keeps it territory during the winter as well (Haftorn 1971). The pied flycatcher is a long-distance migratory species that overwinter in West Africa and breeds in temperate forest in Europe (Lundberg & Alatalo 1992).The males arrive to the breeding grounds about one week before the females, to secure a high-quality territory and ultimately a breeding partner (Lundberg & Alatalo 1992; Both et al. 2016). Early arriving females will have the opportunity to brows the different males, securing a male with good resources (Slagsvold 1976). Timing of arrival is therefore at the up-most importance for the male and the female pied flycatcher. However, arriving too early may reduce survival due to the risk of encountering harsh conditions, whilst arriving too late may reduce reproductive success (Both et al. 2016). It is therefore important to get an understanding on how long-distance migration may influence the pied flycatcher breeding phenology and ultimately their fitness.

For long-distance migratory species, climate change has a different effect than on short-distance and resident species. Short-distance migrating birds are more flexible in their response to temperature, in respects to when they should arrive at breeding grounds (Both & Visser 2001; Smallegange et al. 2010). They are able to use local temperatures at the wintering grounds to adjust and fine-tune the arrival time and onset of egg-laying (Dunn 2004) and often show a trend towards earlier arrival (Walther et al. 2002). Long-distance migratory species on the other hand, show more complex response, with many species not changing their arrival times or even delaying them (Walther et al. 2002; Sanz 2003). The climate at the wintering grounds is not a good prediction for the conditions at the breeding grounds, due to the environmental changes at the wintering grounds and breeding grounds are changing at different speeds (Both & Visser 2001). The most extensive increase in temperature has occurred in the northern latitudes above >50°N (Dunn 2004; Walther et al. 2002), making it even tougher for those breeding in Scandinavia compared to those in Central-Europe.

Long-distance migratory species often rely on endogenous rhythms (Both & Visser 2001), photoperiod (Dunn 2004; Ahola et al. 2004; Walther et al. 2002) or environmental stimuli that are not due to change in temperatures (Ahola et al. 2004) to initiate spring migration. The onset of spring migration is therefore not affected by the changing temperatures, but may cause issues concerning their breeding ecology. The migratory species may arrive too late to take full advantage of changes in food availability (Dunn 2004) and a mismatch, like in the Netherlands (Both et al. 2006), will occur and possibly lead to a reduction in population size (Both et al. 2006). However, during spring migration, temperatures along the migration route, especially at the last stages (Ahola et al. 2004), can influence the speed and the individuals can thereby adjust the arrival time to the breeding grounds (Hüppop & Winkel 2006; Ahola et al. 2004; Both et al. 2005). A new study by Ouwehand and Both (2017) contradict these findings, with results showing no difference in migration time among Dutch pied flycatchers, but rather that the variation in departure date was the cause for variation in arrival date. They also concluded that the variation in departure time depended on age, sex and if the males had previously bred or not.

1.6 Purpose and predictions

As documented in multiple reports (Crick et al. 1997; Crick & Sparks 1999; McCleery & Perrins 1998; Visser et al. 1998; Slagsvold 1976; Matthysen et al. 2011) the response to climate change has varied both among the passerine birds species and within the species, with regards to the degree of advancement of laying dates in relation to increasing spring temperatures. To my knowledge, there are limited studies regarding how increasing temperatures have affected passerine bird species in Norway. I will therefore in this thesis focus on the relationship between annual laying date and spring temperature for four passerine bird species, namely the nuthatch, the blue tit, the great tit and the pied flycatcher, in Norway.

The relationship between laying date of first egg and spring temperature will be examined for each species, and among the species. I will use the variation in mean laying date to evaluate the importance of temperature, exploring both the annually, periodic and long-term variations. Long-term variations in snow depth and precipitation will also be looked into. Since less is known about the nuthatch, additional analysis will be done to see if there is a relationship with altitude above sea level. I will do this by analysing laying dates for individual nest boxes in relation to altitude above sea level. Some of the predictions I have for this study are:

1. The nuthatch will start breeding first, followed by the blue tit, the great tit and lastly the pied flycatcher.
2. Annual variation in mean laying date will have a stronger correlation with ambient temperatures during earlier period of spring for the nuthatch than the three other species, followed by the blue tit, great tit and the pied flycatcher.
3. The correlation between mean laying date and spring temperature will be weaker in the pied flycatcher compared to the others because it is a long-distance migratory specie, arriving late in spring.
4. The annual variation in mean laying date will be positively correlated among the species, and strongest between the blue tit and the great tit, because of similar feeding and breeding ecology.
5. Egg-laying date of individual nuthatches are delayed with increasing altitude, in magnitude similar to the delay of environmental phenology (Slagsvold et al. 2013).

2 MATERIALS AND METHODS

2.1 Study species

The Nuthatch

Nuthatches are easy to recognize- just look for a bird climbing down a tree trunk head first in a zigzag pattern, and there you have it. Their robust feet and strong grasping claws make it possible for their characteristic acrobatics (Haftorn 1971). This enables them to forage on the perimeter of the trunk and branches looking for arthropods, in all forms, especially spiders, caterpillars and beetles (Matthysen 1998). When nuts and seeds are available they will consume this as well or store them for later (Matthysen 1998).Nuthatches prefer to breed in deciduous, high trees and uses large knotholes, cracks or old woodpecker holes as their nesting site (Haftorn 1971; Wesołowski & Rowiński 2004), although nest boxes may be used when available (Enoksson 1993; Haftorn 1971). The nest consists of ample amounts of bark flakes and a thick layer of plastered, wet clay surrounds the entrance hole (van Balen et al.1982; Haftorn 1971; Wesołowski & Rowiński 2004). Plastering the entrance hole, making it narrower, is to protect against predators and competition from other species (van Balen et al. 1982). The bark is collected from tree trunks and is therefore available before the snow has melted. However, clay has to be collected from the ground and is dependent on time of snow melting. The nuthatches are very territorial and will stay all through the year at their nesting site with their paired mate (Matthysen 1998).

The Blue Tit

The blue tits inhabit deciduous and mixed forest in the lowlands of Norway and are quite an abundant passerine species (Haftorn 1971). Cavities in threes and nest boxes are the most used nest sites, where they use moss, wool, hair and feathers as nesting material. Both moss and lining for the nest is collected from the ground and they are therefore dependent of bare grounds to start nest building. They are known to lay rather large clutches ranging from 3- 16 eggs, of which they are very protective off. During summer, their diet consists mostly of insects, spiders, aphids, butterfly larvae and pupae, whilst during the winter, seeds and berries from evergreens are consumed (Haftorn 1971).

The Great Tit

The great tit is among the most abundant passerine birds in Norway and widespread across the country in all types of forest (Haftorn 1971).They breed in cavities in tress, natural cavities and high proportion breed in nest boxes when available. Nests are made with large amounts of moss as the base layer with the addition of wool, threads and hair. Both moss and lining for the nest is collected from the ground and they are therefore dependent of bare grounds when constructing their nest. Insects and spiders are their main food resource during summer, while during winter pine seeds and bird seeds from local settlement dominate. Butterfly larva are the nestling’s main food recourse often only available for a short time during spring (Perrins 1965). Some short-distance migration during winter occur among the juveniles, while adults, in our study site, stay at the breeding ground all year round (T. Slagsvold per. com.)

The Pied Flycatcher

The pied flycatcher is a long-distance migratory species which overwinters in West Africa, south of the Sahara desert, where the climate is dry tropical forest (Lundberg & Alatalo 1992; Sanz 2003). In early May, they return to their breeding grounds in Norway and start looking for nest site. The nesting site can be a natural hole or a nest box, re-using abandoned nests from other species occurs often (Haftorn 1971). Nest material is composed of dry leaves, bark and straw, either on top of an existing nest or in a new, empty hole (Haftorn 1971). Their diet consists mostly of prey from the Hymenoptera order (ants, bees, wasps) and beetles, with the addition of butterflies and their larvae for nestling food (Lundberg & Alatalo 1992).

2.2 Study area

The study area used for this thesis has been used since 1995 for different projects concerning passerine birds. The study area encompasses 1.6km^2 located at Dæli (59°56’N, 10°32’E) around 10km from Oslo, Norway. The study area is situated by the Dælivannet and is part of a large area of woodland, with settlement and farmland intertwined. The woodland is dominated by deciduous trees, but some scattered coniferous trees such as Norway Spruce *Picea abies* and Scotch Pine *Pinus* *sylvestris* are found alone or in patches (Slagsvold et al. 2013). Among the most common deciduous trees in the area are European Ash *Fraxinus excelsior*, Hazel *Corylus acellana*, Norway Maple *Acer platanoides*, Eurasian Elm *Ulmus glabra*, birch *Betula spp.* and willow *Salix spp.* (Slagsvold et al. 2013).

Approximately 500 nest boxes have been available every year and are scattered around in the study area among the different habitats. The coordinates and elevation of each nest box is know from GPS recordings by Slagsvold et al. (2013) and are dispersed in altitudes ranging from 105 to 266 m a.s.l. The annual spring occupancy of breeding pairs in the nest boxes are on average ~9 for the nuthatch, ~70 blue tit, ~95 great tit and ~60 pied flycatcher. However, the nuthatch has the last couple of years more than doubled in breeding pairs in our area (appendix table 1).

2.3 Weather and Climate data

The entire climate data used in this thesis was obtained from the Norwegian Meteorological Institute (eklima 2016). I collected data from two different meteorological stations, Blindern and Horni. The mean and max daily spring temperatures were obtained from Blindern meteorological station, located 15km from the study area. Even though Blindern meteorological station is located a bit away from the study area, this station is the only one with similar altitude (96 m a.s.l) as the study area, and has a detailed timeseries regarding temperature which is needed for doing the analysis. The mean daily precipitation and snow depth were measured at Horni meteorological station (81 m a.s.l) located 5km from the study area. I chose to use Horni for precipitation and snow depth due to the fact that Horni is a more rural area compared to Blindern, and would therefore give a more realistic comparison of the conditions at the study area.

2.4 Data collection

The data collected are from a 14-year period, 2003-2016, where I contributed with fieldwork in April-June 2016.

All nest boxes were visited at least once a week from the start of April to take notes on whether any nest building had started or if they were still vacant. Each time a nest box was visited, we recorded how far the nest building had come and what type of nest material was used. At the time of nest completion, visitation became more frequent and during the most important pre-laying period, nest boxes were visited more often. We have assumed, like previous studies (Crick et al. 1997; Matthysen et al. 2011; Hinks et al. 2015), that one egg was laid every day (Perrins 1970). However this does not take into account laying interruptions (Matthysen et al. 2011) due to temperature change. To determine a more precisely laying date for first egg, nest boxes were visited at least every other day during the most critical period. This way we would be able to have a much more precis time of first egg laid. The laying dates are used to calculate the mean laying date of each year, which is the average for all first clutches (the first clutch that a female produces in that year). Sometimes first clutches fail, resulting in production of replacement clutches. Replacement clutches, second clutches and data from cross-fostered females were excluded from this study. This we can be sure of because the local recruits are ringed from previous years, and new recruits are caught and ringed once they have settled in a nest box.

2.5 Statistical analyses

All statistical analysis were performed using the statistical computer software R 3.3.1 (R Core Team, 2016) and RStudio (RStudio© inc. 2016). Diagrams, figures and tables were produced in Excel© 2013 for Windows.

For each of the four species number of nests, mean laying date, standard deviation (SD), standard error (SE) and mean SE, for each year, was calculated (appendix table 1). An additional data set was made for the nuthatch where the recorded laying date, altitude, longitude and latitude for each nest box, each year was entered.

The mean daily temperature for the period 1 March to 18 June was used for all calculations. I further sub-divided the time series into 20-day periods where each period had a 10-day overlap (Slagsvold 1976). The mean temperature for each 20-day period per year are calculated in RStudio (2016) (appendix table 2). These data are further used in RStudio (2016) where Pearson’s correlation was used to calculate the correlation coefficient for each period against mean laying date, for each species, to find the most important pre-laying period (Slagsvold 1976). Significance and regression equation were calculated using R Linear model function summary.
To see whether the amount of precipitation, temperature or snow depth has changed significantly the last 14 years, correlation, p-value and regression equation were calculated for each month using R Linear model function summary.

The interrelationship between spring warmth sum and mean laying date of first egg shows if the birds are adjusting laying date to spring temperature. For the calculations on warmth sum I followed McCleery and Perrins (1998) and Charmantier et al. (2008), procedure and calculated warmth sum as the sum of the daily maximal temperature from 1 March to 30 April in each year. This time period was used for the nuthatch, blue tit and great tit. Since the pied flycatcher usually does not arrive in Norway before sometime in April, I used an additional maximal temperature from 1 April to 30 May, which is more relevant, in accordance to their laying date. Pearson's product-moment correlation was used to calculate the relationship between warmth sum and mean laying date of first egg.

To test the temperature hypothesis used by Visser et al. (2003), I used the mean laying date from 2003-2016 to find a collective mean laying date throughout the period separately for each species. I chose not to use a fixed laying date for all species collectively, since the mean laying dates are not significantly correlated (table 2). Pre-laying temperature was calculated as the mean temperature in the six-week period prior to the mean laying date. The breeding temperature was calculated as the mean temperature in the four-week period succeeding the mean laying date. These calculations were done for each individual year and species. Pearson’s product-moment correlation and R Linear model function summary were used to determine changes in the pre-laying and breeding period for each species.

3 RESULTS

3.1 Mean values and long-term changes in laying date and weather conditions

Mean date of first egg (calculated as mean of the annual mean values) was 20 April for the nuthatch, 1 May for the blue tit, 3 May for the great tit and 23 May for the pied flycatcher (figure 2). Laying date has not advanced over the last 14 years, 2003-2016, for either of the four species (figure 3, table 1a). The temperature, snow depth and precipitation have also not significantly changed over the last 14 years (table 1b-d).

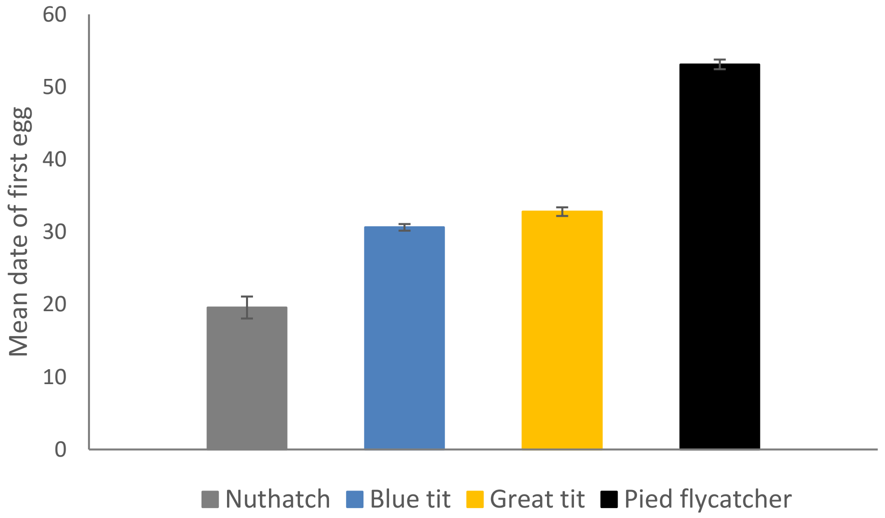

Figure 2. The mean date of first egg with mean SE (1 = 1 April, calculated as mean of the annual mean values) during the period 2003-2016, for the nuthatch, blue tit, great tit and the pied flycatcher.

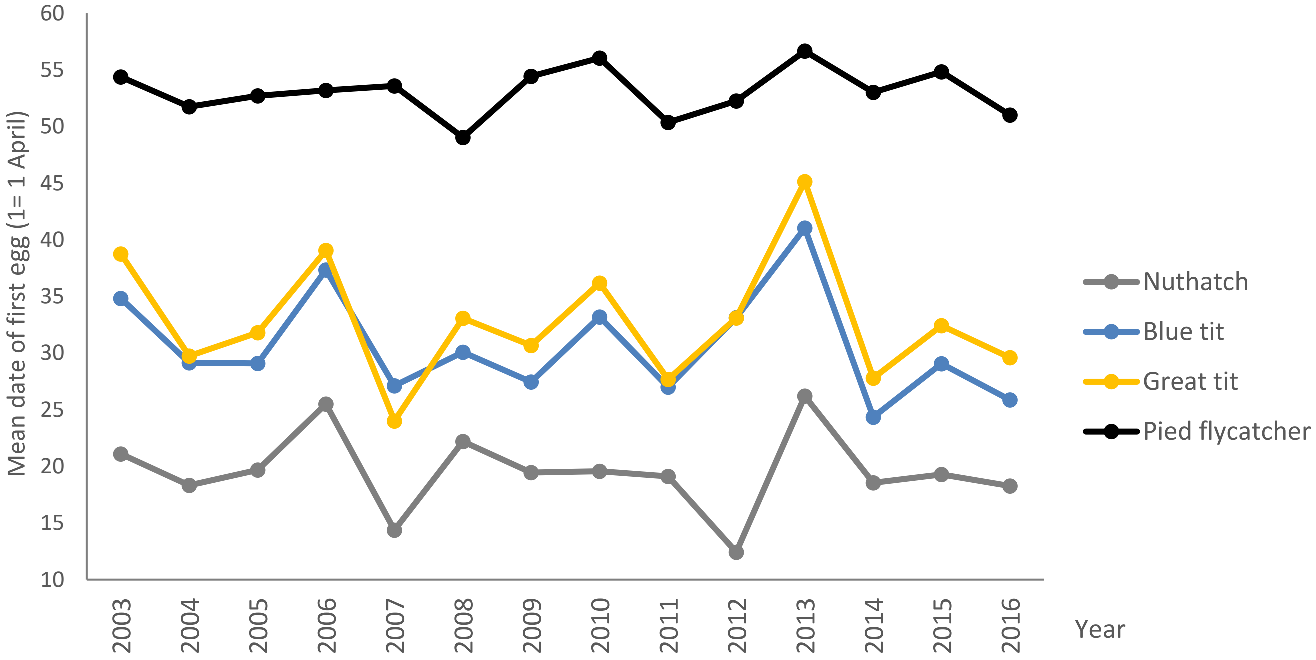

Figure 3. Annual mean laying date of first egg (1 = 1 April) for the nuthatch, the blue tit, the great tit and the pied flycatcher.

Table 1. Correlations between annual **(a)** mean laying date for first egg, **(b)** mean temperature (°C), **(c)** mean snow depth (mm), and **(d)** mean precipitation (mm) and year (N = 14). The respective regression equations are showing the laying date (1 = 1 April) (a), and climatic factors (b-d), as a function of year.

Species	r	p	Regression equation
(a) Laying date			
Nuthatch	-0.12	0.67	-0.110x + 239.6
Blue tit	-0.21	0.47	-0.237x + 507.3
Great tit	-0.08	0.78	-0.107x + 247.3
Pied flycatcher	0.07	0.81	0.036x - 18.5
(b) Temperature			
March	0.34	0.24	0.203x – 406.8
April	-0.05	0.86	-0.017x + 41.1
May	0.18	0.54	0.049x – 88
(c) Snow depth			
February	-0.26	0.37	-1.401x + 2855.0
March	-0.32	0.26	-1.793x + 3635.7
April	-0.31	0.30	-0.666x + 1345.6
(d) Precipitation			
March	0.046	0.88	0.01x – 19.1
April	-0.044	0.88	-0.009x + 20.6
May	0.22	0.46	0.066x – 129.5

The annual variation in mean laying date and year (2003-2016) was positively correlated between the species, with the correlation between the blue tit and the great tit being the strongest (table 2). There was a significant difference in laying date between all the species (table 2).

Table 2. Difference (calculated with paired sample t-test with 95% confidence interval) and correlation in annual mean laying date between the species.

		t-test between means		**Correlation between species**	
Species 1	**Species 2**	**t**	**p**	**r**	**p**
Nuthatch	Blue tit	10.59	< 0.001	0.59	0.03
Nuthatch	Great tit	13.01	< 0.001	0.73	0.003
Nuthatch	Pied flycatcher	33.49	< 0.001	0.24	0.42
Blue tit	Great tit	4.02	0.002	0.93	< 0.001
Blue tit	Pied flycatcher	20.52	< 0.001	0.50	0.07
Great tit	Pied flycatcher	15.95	< 0.001	0.52	0.06

Annual mean laying date of first egg was negatively correlated to spring warmth sum for three of the species (table 3). In years where temperatures were high, they laid earlier, than in years when the temperature was low. The interrelationship between mean laying date and warmth sum was highly significant for the nuthatch (p = 0.003), the blue tit (p = 0.05) and the great tit (p = 0.028). The pied flycatcher did however not lay significantly earlier in response to higher temperatures (p = 0.55). For the latter species, the warmth sum period from 1 April to 30 May gave a stronger correlation than the 1 March to 30 April period , but still not significant (p = 0.45) (table 3).

Table 3. Relationship between spring warmth sum and mean laying date of first egg for 2003-2016 (N = 14). The warmth sum is calculated as the sum of daily maximum temperatures from 1 March to 30 April in each year. The respective regression equations are showing the laying date (1 = 1 April) as a function of temperature.

Species	**r**	**p**	**Regression equation**
Nuthatch	-0.73	0.003	-0.0184x + 28.8
Blue tit	-0.53	0.05	-0.0173x + 39.4
Great tit	-0.59	0.028	-0.0223x + 44.0
Pied flycatcher	0.18	0.55	0.0026x + 51.8
Pied flycatcher *	0.22	0.45	0.0051x + 48.8

* warmth sum period from 1 April to 30 May.

Neither the six-week pre-laying period, nor the four-week breeding period had significantly changed in temperature the last 14 years for either of the four species (table 4).

Table 4. Significance of temperature during **(a)** pre-laying period, the six week prior to the mean laying date and **(b)** breeding period, four week period post the mean laying date, in the years 2003-2016 for each individual species.

Specie	r	p
(a)		
Nuthatch	0.17	0.58
Blue tit	0.02	0.96
Great tit	-0.003	0.99
Pied flycatcher	-0.10	0.74
(b)		
Nuthatch	-0.26	0.37
Blue tit	0.11	0.70
Great tit	0.19	0.52
Pied flycatcher	0.14	0.62

3.2 Influence of temperature on annual variation in mean laying date

The correlation between annual mean laying date and temperature, varied both among the four species and the various periods in spring (figure 4, statistics see appendix table 3). For the nuthatch, the correlation between the mean laying date and temperature was highly correlated for the periods 11-30 March ($r = -0.90$, $p < 0.001$) and 21 March-9 April, with the latter being slightly stronger correlated ($r = -0.91$, $p < 0.001$, figure 5a). For the blue tit and great tit the onset of laying was closely related to temperature from the 1 March and continuously strengthened until the strongest negative correlation was obtained in the period 31 March-19 April (blue tit $r = -0.82$, $p < 0.001$; great tit $r = -0.80$, $p < 0.001$, table 5, figure 5b,c). In the following period, the correlation weakened but was still significant until the 20 April-9 May period. For the pied flycatcher on the other hand, laying date was only correlated to the period 20 April-9 May (r = -0.65, p = 0.012, table 5, figure 5d). The most important pre-laying period for each individual specie ended ~10 days before the mean laying date.

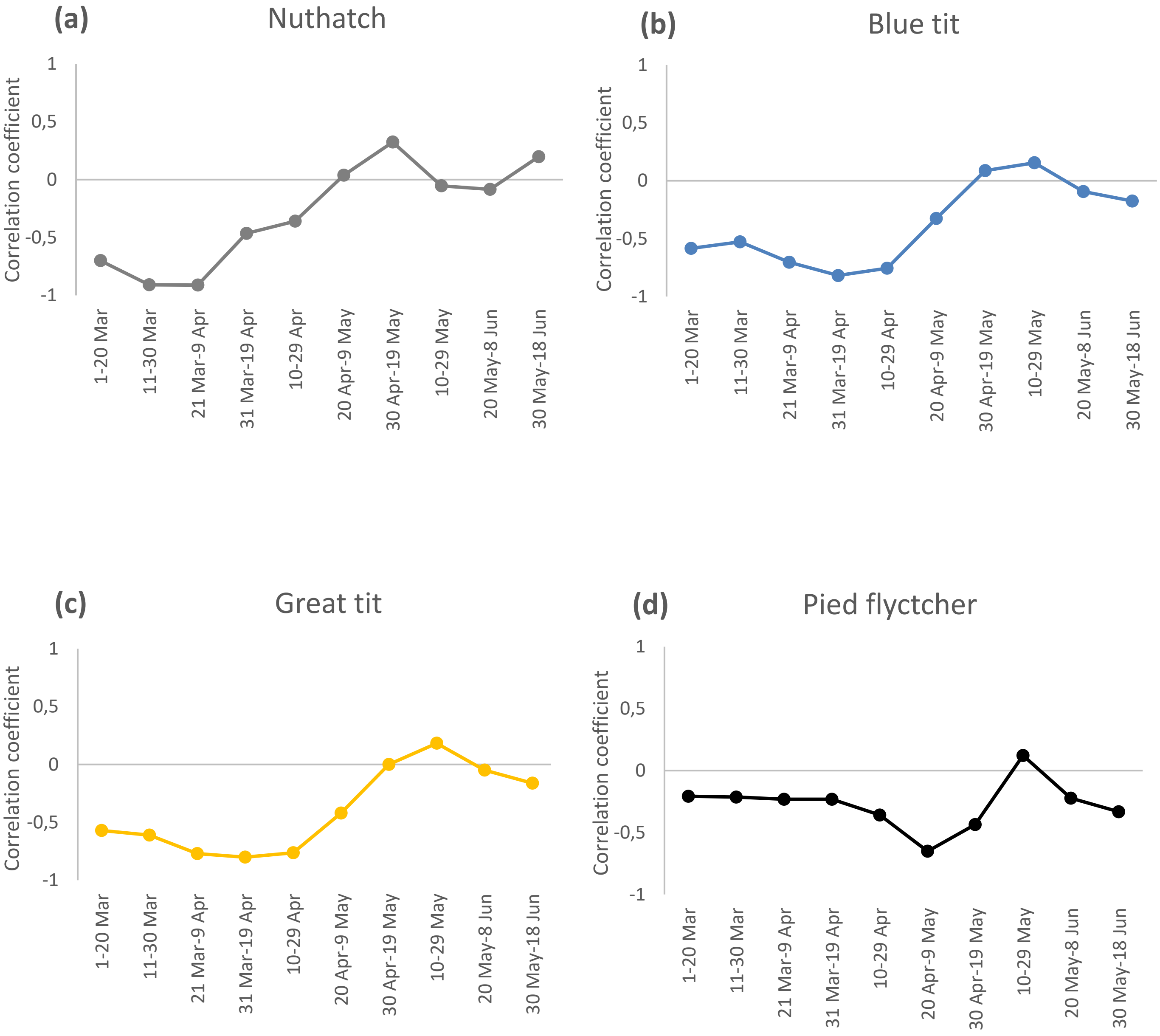

Figure 4. Variation in the correlation coefficient between annual mean temperatures during various 20-day periods in spring. Correlation coefficient is calculated as the mean date of first egg in each year (N = 14, 2003-2016) against each individual period (N = 10), separately for the four species.

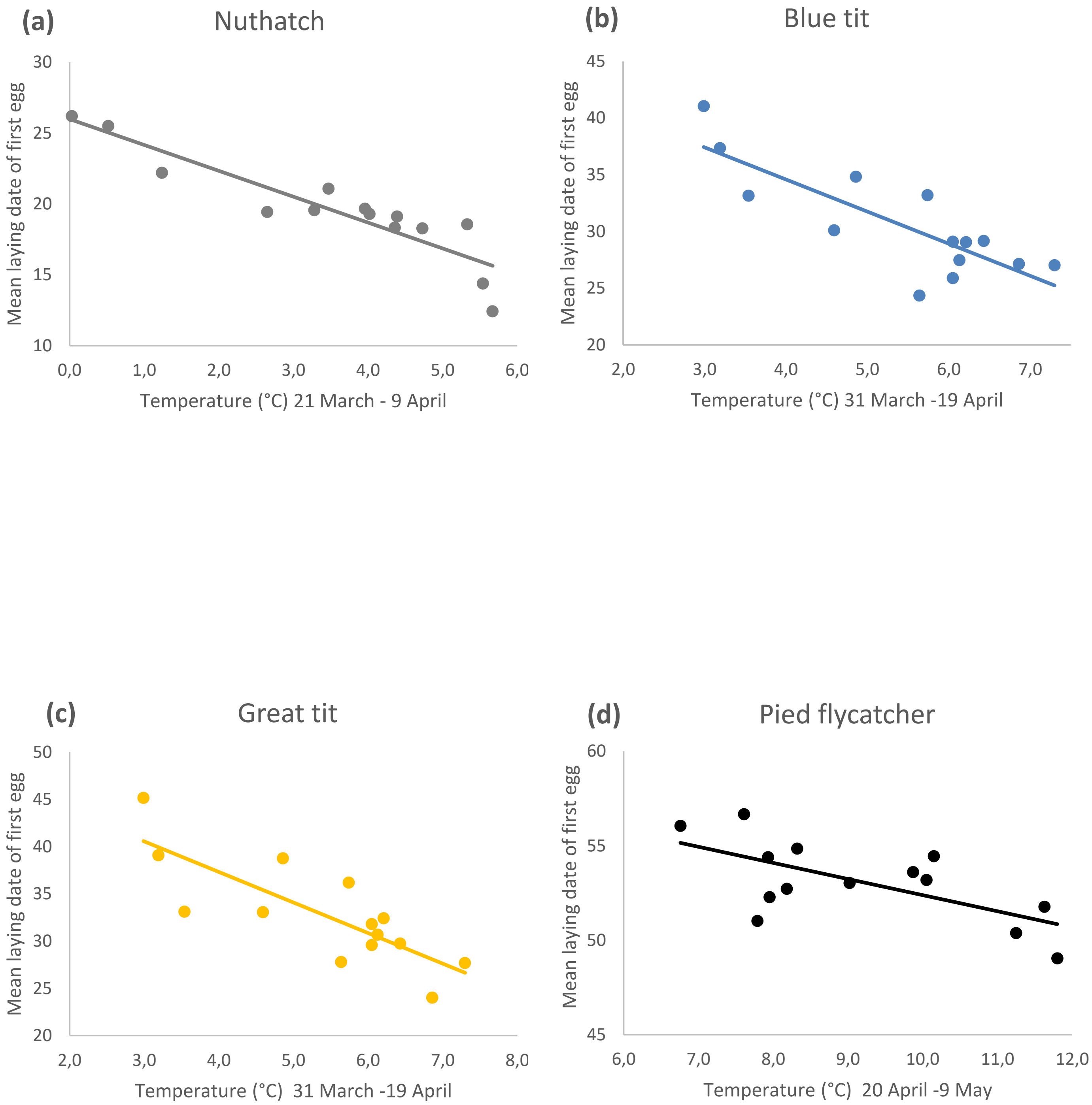

Figure 5. The species-specific pre-laying periods whose temperature best explained the annual mean laying date for the years 2003-2016 (N = 14). For statistics, see table 5.

Table 5. Statistical analyses from the specie-specific pre-laying period that gave the highest correlation in relation to annual mean laying date. The respective regression equations are showing the laying date (1 = 1 April) as a function of temperature.

Species	**Pre-laying period**	**r**	**p**	**Regression equation**
Nuthatch	21 March – 9 April	-0.91	< 0.001	-1.83x + 26.0
Blue tit	31 March – 19 April	-0.82	< 0.001	-2.83x + 45.9
Great tit	31 March – 19 April	-0.80	< 0.001	-3.23x + 50.3
Pied flycatcher	20 April – 9 May	-0.65	0.012	-0.85x + 60.9

3.3 Laying date of nuthatch in relation to altitude

Date of first egg in individual nests by nuthatches during 2003-2016, in relation to altitude above sea level of the nest box (figure 6). There is a significant relationship between the laying date and the altitude of the nest box used. Per 100m increase in altitude, there was approximately a two-day delay in laying date.

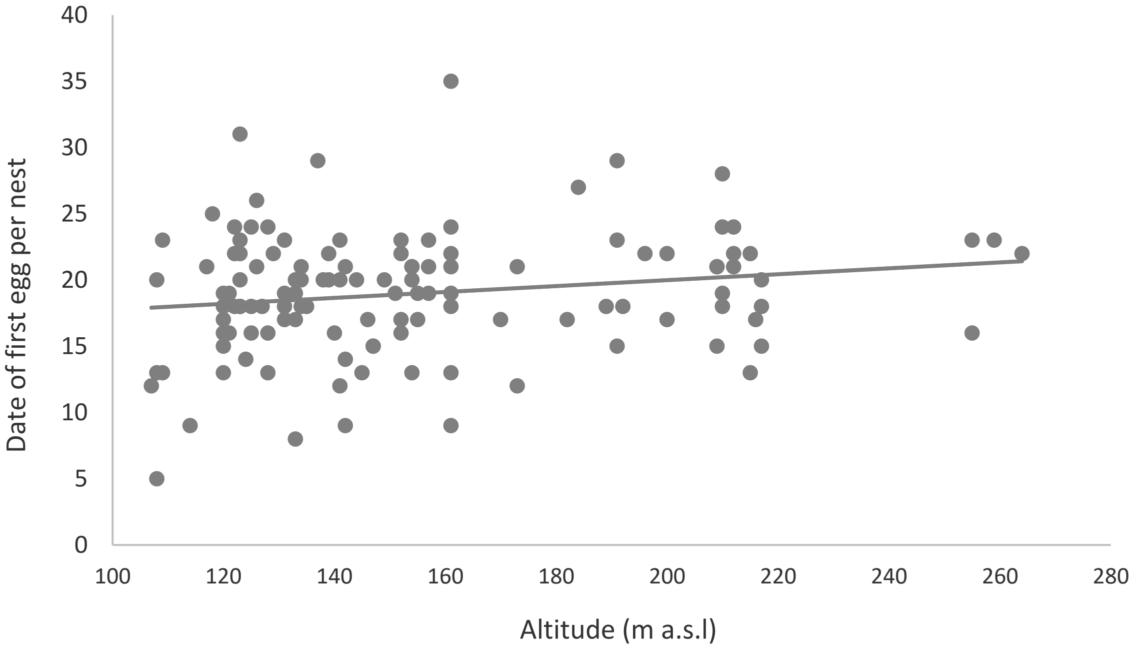

Figure 6. Date for first egg for the nuthatches in relation to altitude (m a.s.l) of all individual nest boxes used by the species during 2003-2016. The delay is of approx. two days per 100m increase in altitude ($y = 0.022x + 15.5$, $n = 121$, $r = 0.18$, $p = 0.05$).

4 DISCUSSION

There is a short period during the year where the conditions are most favourable for breeding. This period varies from year to year, due to fluctuations in the environment. Temperatures during spring is the main climatic factor influencing the phenology of organisms (Walther et al. 2002). The results from this thesis, show that there has not been an advancement in annual mean laying date for neither the nuthatch, the blue tit, the great tit nor the pied flycatcher. Annual spring temperature, precipitation nor snow depth has significantly changed during 2003-2016. The species are however, to various extent, able to adjust annual laying date to the temperature experienced during early spring, laying earlier in years with warmer spring temperatures. The pied flycatcher is the specie that has the weakest correlation between laying date and spring temperature. This is probably a result of arriving late to the breeding grounds from wintering grounds in Africa.

4.1 Long-term changes

The global average temperature has increased by 0.85 °C (IPCC 2013). The mean monthly temperature, at my study area, has however not significantly increased the last 14 years, nor has mean precipitation or mean snow depth. When considering the global increase in temperature, I would have expected an increase in spring temperature at the study area. The reason why no significant change in temperature has occurred can be that the number of years used in the study is not substantial enough. However, my results above comply with the mean laying date of first egg has not significantly advanced for the four study species the last 14 years. Nevertheless, there has been a slight shift towards advancement in laying date with regard to the nuthatch, the blue tit and the great tit, although not significant. This is in marked contrast to other studies in the UK and Belgium, where the mean laying date and caterpillar abundance has advanced significantly due to increased spring temperatures (van Noordwijk et al. 1995; Crick et al. 1997; Visser et al. 2003).

To understand why laying date has not advanced I tested Visser et al. (2003) temperature hypothesis to see whether there had been an increase in temperature during shorter periods, that may have affected different stages of the breeding cycle. The increase in spring temperature might have occurred only for the period in spring after the birds have already started laying, and not in the pre-laying period. The results conclude that an increase in spring temperature has not occurred during the six-week pre-laying, nor the four-week breeding period, for any of the species. This is not surprising given that the mean temperatures in the spring months have not significantly increased.

4.2 Annual variation

Even though the laying date has not advanced, the nuthatch, the blue tit and the great tit are adjusting their annual laying date in relation to spring temperature. In years with high spring temperatures the mean laying date is correspondingly earlier, and vice versa when spring temperatures are low (e.g Perrins & McCleery 1989). This shows that the three species are able to track annual spring temperature and adjust accordingly. There would be no need to advance their laying date if the spring temperature is not advancing. The main reason for advancing laying date is to match the peak of food abundance. Since the peak of food abundance is closely related to temperature (Both & Visser 2005), I would presume that the three species are able to match the peak food abundance. Whether or not the peak food abundance has advanced in the area during 2003-2016 is unknown, but by looking at previous published material (Slagsvold 1976) from the same area, annual variation in mean laying date of the great tits closely followed the tree phenology with respect to the temperature experienced. This was however the situation 40 year ago. As previously mentioned, the global temperature increase has accelerated after the 1970s (Walther et al. 2002). Thus, the situation might not be the same today, and further analyses with regard to tree phenology and food abundance, needs investigating. Although looking at the overall results from this thesis, it seems that the nuthatch, the blue tit and the great tit are able to adjust to the variation in annual spring temperatures and that the low occurrence of failed nests (pers. com. T. Slagsvold) substantiate that they are able to match the peak of food abundance.

The temperature during spring has an effect on the timing of breeding as we have seen. Knowing how temperatures in various period during spring is related to the onset of egg-laying, is therefore important. All of the species have a specie-specific 20-day period where the correlation between mean laying date and temperature were highly significant. These most important pre-laying periods may work as cues for when to initiate the breeding cycle. For all of the four species, mean laying date for each species occurred ~10 days after the end of their most significant 20-day temperature period. The most important pre-laying temperature period is, as expected, some days before the annual mean laying date, because time is needed for nest completion and gonad development, which takes about four days (Perrins 1996)

4.3 Relation to altitude

For the nuthatch, the relationship between the altitude of individual nest boxes and laying date of first egg in each individual nest box throughout the 14-year period, showed that there was a delay in laying date by two days per 100m increase in altitude. This is in accordance to the delay of birch phenology in the same area (Slagsvold et al. 2013; Hušek et al. 2014). This further supports the notion that the nuthatch most likely adjust the laying date with spring temperature and tree phenology.

4.4 Comparisons between the species

As predicted, the annual variation in mean laying date had a stronger correlation with temperatures during the earlier periods of spring for the nuthatch than the three other species, followed by the blue tit, great tit and the pied flycatcher. This is reflected in the time of egg-laying, where the nuthatch started breeding first among the four species, with the mean laying date of first egg being on the 20 April. The blue tit and great tit follow 1.5 weeks later with mean laying date of first egg being 1 May and 3 May, respectively. The laying date, for the latter two, are similar throughout the years, with the blue tit laying a couple of days earlier than the great tit. This is as predicted, i.e. the blue tit and great tit annual mean laying date will be positively correlated because of the similarities in their feeding and breeding ecology (Haftorn 1971). The blue tit and the great tit are more dependent of snow clearance to be able to find nesting material on the ground, and the emergence of caterpillar prey, than the nuthatch. The nuthatch uses bark from tree trunks as nesting material, and it has also a wider array of prey specimen to utilize. This makes it possible for the nuthatch to start breeding earlier than the tits. The pied flycatcher on the other hand does not start egg-laying until the end of May, with mean laying date on 23 May. The annual mean laying date of pied flycatcher was rather predictable being relative constant on the 23 May +/- 3 days. This is in distinct contrast to the tits where the laying date between years may vary as much as 20 days. The relative constant laying date of the pied flycatcher can be explained by it being a long-distance migratory species, who relies on endogenous rythms (Both & Visser 2001) to initiate migration. Their late spring arrival time to the breeding grounds are thereby not influenced by the fluctuations in the early spring temperatures as for the three other species. This is also evident when looking at the annual variation in mean laying date in relation to spring temperatures. The correlation between mean laying date and mean temperature during various spring periods are weaker in the pied flycatcher compared to the three other species. The pied flycatcher mean laying date was only significantly correlated with one temperature period during spring (appendix table 3).

The arrival date is to a large extent determined by the date of departure from the wintering grounds in Africa, but also to the conditions they encounter during migration. There is some debate on whether temperature conditions encountered during the migration route can alter the individual's speed, and thereby arriving earlier at the breeding grounds. Ouwehand and Both (2017) show that there is no difference in migration time, stating that the departure time from the wintering grounds is the ultimate factor in determining arrival time at breeding grounds. These findings are in contrast to other studies (e.g. Ahola et al. 2004; Hüppop & Winkel 2006; Both et al. 2005) that found that temperature encountered during migration would affect their speed and thereby advancing arrival time at the breeding grounds. The study by Ouwehand and Both (2017) is still in its early stages, but their method of using geolocators to track an individual's movements more precisely, rather than following population movements. Further research is thus needed to be able to conclude which factors determine and affect the arrival date at breeding ground.

4.5 Further studies

Much has been done in regard to studying the phenology of the great tit, the pied flycatcher and to some extent the blue tit, in certain parts of Europe. However, more studies are needed to map the variation between different geographical regions in Europe and how various populations are responding to climate change. Meta-analysis like those by Visser et al. (2003) and Sanz (2002) gives us an insight into the wide array of limitations and adaptions among different species, making it easier to predict the future for passerine birds. Not much is known about the breeding phenology of the nuthatch, and in particular to which extent their phenology is affected by climate change. The challenge with studying the nuthatch breeding phenology is due to their breeding habit, using natural cavities, and not nest boxes, often being 10m above ground. However, since 2015 the number of nuthatches using the nest boxes in our study area for breeding, has increased dramatically (appendix table 1). From 2004-2014 there were on average 6 nest boxes used by breeding nuthatches, whilst the two last years (2015-2016) had respectively 17 and 25 nest boxes used by breeding nuthatches. We do not know if this is related to an increase in population size, inheritance or preference over natural cavities. There is ample of work to be done on all species, and I hope that the nuthatch gets extra attention.

For the pied flycatcher, further studies are needed so that we can understand which mechanisms that determine the arrival date at the breeding ground. At our study area it would be beneficial to look into the time elapsing from the arrival date and until the first egg is laid. Has there not been an advancement in laying date due to the timespan after arrival cannot be reduced, or is the current mean laying date suitable in relation to the peak of food abundance?

In this thesis, I have only scratched the surface of understanding the breeding phenology of four passerine bird species here in Norway. I have shown that they are able to adjust breeding time to earliness of spring. Looking into number of clutches, clutch size and fledgling success might help us to understand how temperature is affecting different aspects of their breeding phenology. This of course needs to be seen in perspective to other trophic levels. Measurements of the tree phenology and food abundance during the spring will shed light on how climatic conditions are affecting different trophic levels and ultimately the birds breeding phenology.

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6 APPENDIX

6.1 Appendix 1. Annual laying date

Appendix table 1. Overview of the annual mean laying date of first egg (1.egg), number of nests (N), standard error (SE) and standard deviation (SD) for each of the individual four species in the period 2003-2016 (N = 14).

	(a) Nuthatch				**(b)** Blue tit				**(c)** Great tit				**(d)** Pied flycatcher			
Year	**1.egg**	**N**	**SE**	**SD**	**1.egg**	**N**	**SE**	**SD**	**1.egg**	**N**	**SE**	**SD**	**1.egg**	**N**	**SE**	**SD**
2003	21.1	12	1.2	4.1	34.8	86	0.83	7.7	38.8	62	0.88	6.9	54.4	75	0.45	3.9
2004	18.3	3	1.8	3.1	29.2	77	0.63	5.5	29.8	57	0.63	4.8	51.8	76	1.03	9.0
2005	19.7	3	1.9	3.2	29.1	80	0.56	5.1	31.8	54	0.76	5.6	52.7	49	0.71	5.0
2006	25.5	2	1.5	2.1	37.4	69	0.37	3.1	39.1	60	0.42	3.2	53.2	69	0.80	6.6
2007	14.4	8	1.2	3.4	27.1	107	0.48	5.0	24.0	81	0.57	5.1	53.6	60	1.01	7.8
2008	22.2	5	2.1	4.7	30.1	92	0.38	3.6	33.1	72	0.50	4.2	49.0	54	0.80	5.9
2009	19.4	9	0.9	2.7	27.5	95	0.38	3.7	30.7	63	0.41	3.3	54.4	52	0.81	5.8
2010	19.6	7	2.1	5.5	33.2	116	0.35	3.8	36.2	67	0.65	5.4	56.1	56	0.59	4.5
2011	19.1	9	1.1	3.2	27.0	109	0.34	3.6	27.7	80	0.44	3.9	50.4	77	0.56	4.9
2012	12.4	7	2.0	5.4	33.1	111	0.36	3.8	33.1	91	0.51	4.9	52.3	62	0.43	3.4
2013	26.2	5	2.5	5.5	41.0	106	0.33	3.4	45.2	82	0.55	5.0	56.7	62	0.64	5.1
2014	18.6	9	1.6	4.9	24.4	80	0.27	2.4	27.8	80	0.53	4.7	53.0	61	0.41	3.2
2015	19.3	17	0.8	3.1	29.1	104	0.52	5.3	32.4	75	0.78	6.8	54.8	50	0.51	3.6
2016	18.3	25	0.7	3.6	25.9	90	0.57	5.4	29.59	76	0.70	6.1	51.0	46	0.55	3.7

6.2 Appendix 2. Mean ambient air temperature (°C)

Appendix table 2. The mean annual spring temperature for each 20-day period, with a 10-day overlap between the periods, for the years 2003-2016. The mean annual temperatures are calculated from mean daily temperatures.

	Mean spring temperature (°C)														
20-day period	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**Mean period**
1-20 March	0.6	1.2	-3.1	-4.8	3.1	2.0	1.3	-0.8	-0.7	3.8	-2.4	3.6	4.0	2.5	**0.7**
11-30 March	3.3	3.1	0.1	-1.2	5.2	0.3	1.2	1.9	1.4	7.5	-3.1	4.5	3.4	4.3	**2.3**
21 Mar. -9 Apr.	3.5	4.4	4.0	0.5	5.5	1.2	2.7	3.3	4.4	5.7	0.0	5.3	4.0	4.7	**3.5**
31 Mar. -19 Apr.	4.9	6.4	6.1	3.2	6.9	4.6	6.1	5.7	7.3	3.5	3.0	5.6	6.2	6.1	**5.4**
10-29 April	7.1	8.4	7.7	5.6	8.8	7.6	8.9	6.5	10.6	6.1	5.2	9.1	7.8	6.3	**7.5**
20 Apr.-9 May	7.9	11.6	8.2	10.1	9.9	11.8	10.2	6.8	11.3	8.0	7.6	9.0	8.3	7.8	**9.2**
30 Apr.-19 May	8.5	12.9	8.8	12.4	10.1	11.7	10.7	9.4	11.3	9.2	10.8	9.0	8.4	11.2	**10.3**
10-29 May	10.6	11.3	10.2	11.3	10.6	11.0	12.2	12.3	11.7	13.9	13.9	14.0	9.5	12.4	**11.8**
20 May-8 June	14.4	12.8	11.2	12.3	14.6	16.5	13.6	14.7	13.8	14.8	15.1	16.7	10.9	15.9	**14.1**
30 May-18 June	16.1	14.8	12.4	16.0	17.1	17.8	13.7	15.0	15.5	12.4	15.0	17.4	12.9	17.2	**15.2**

6.3 Appendix 3. Influence of temperature on annual variation in mean laying date

Appendix table 3. The relationship between mean annual laying date and mean annual temperature within individual 20-day periods for the years 2003-2016. The species-specific pre-laying periods whose temperature best explained the annual mean laying date is 21 March-9 April for the nuthatch, 31 March-19 April for both blue tit and great tit, and 20 April-9 May for the pied flycatcher.

Species		**1-20 March**	**11-30 March**	**21 March-9 April**	**31 March-19 April**	**10-29 April**	**20 April-9 May**	**30 April-19 May**	**10-29 May**	**20 May-8 June**	**30 May-18 June**
Nuthatch	**r**[a]	-0.7	-0.90	-0.91	-0.47	-0.36	0.038	0.32	-0.054	-0.085	0.20
	p	0.005	< 0.001	< 0.001	0.094	0.21	0.90	0.26	0.86	0.77	0.50
Blue tit	**r**[a]	-0.58	-0.53	-0.70	-0.82	-0.76	-0.33	0.087	0.16	-0.094	-0.18
	p	0.028	0.052	0.005	< 0.001	0.002	0.26	0.77	0.60	0.75	0.55
Great tit	**r**[a]	-0.57	-0.61	-0.77	-0.80	-0.76	-0.42	< -0.001	0.18	-0.048	-0.16
	p	0.034	0.021	0.001	< 0.001	0.002	0.14	0.99	0.53	0.87	0.58
Pied flycatcher	**r**[a]	-0.21	-0.21	-0.23	-0.23	-0.36	-0.65	-0.44	0.12	-0.22	-0.33
	p	0.48	0.46	0.43	0.43	0.21	0.0120	0.12	0.68	0.44	0.25

[a] : Pearson’s product moment correlation coefficient