Nestling Diet Differences between Blue Tits (*Cyanistes caeruleus*) and Great Tits (*Parus major*) in Relation to The Caterpillar Peak and Date

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Abstract

Caterpillars fluctuate throughout the years causing differences in the peak height of caterpillar biomass and the peak date. It is expected that this affects the behaviour of blue tits and great tits during the time they have nestlings. This study aimed to see the change in their nestling diet in terms of the number, type and size of prey in response to between-year variations in the caterpillar peak date and height. Furthermore, we investigated the difference between the species in the number of prey per trip and biomass per chick per hour. This was accomplished via photo analysis of diet sessions, collecting frass under three oak trees and measuring self-caught caterpillars. Paired analyses of 11 great-blue tit nests collected in six years revealed that the average caterpillar biomass and caterpillar biomass per chick per hour were significantly higher for great tits than for blue tits. Most of the blue tits (83%) brought at least once more than one prey per trip. More prey per trip was negatively correlated with the size of caterpillars in blue tits. The number of brought-in prey per hour compared to the caterpillar peak height doesn't show a correlation for both species. The main caterpillar families brought in by the species are Geometridae, Tortricidae and Noctuidae, however, there is a large group of unknown caterpillars. The caterpillar peak date has a significant correlation with caterpillar percentage and caterpillar per hour for blue tits, additionally, caterpillar per hour and prey per hour vary significantly between blue and great tits. We saw no significant correlation compared to the caterpillar peak height, but with more data, this could change. So there is a change in size and number of prey between the species but there is no relation with the caterpillar peak height only with date.

Introduction

In forests, the amount of caterpillars varies strongly between years, which is the main food source of great tits and blue tits (Navalpotro et al., 2016). The caterpillars can peak earlier or later in the spring, depending on temperature, and the amount of caterpillars cycles with a periodicity of approximately ten years (Nadolski et al., 2021; Fig. 1). Caterpillars have to grow quickly to eat the young leaves of the trees and afterwards become pupae (Both et al., 2009). Winter moth caterpillars change from larvae to pupae within approximately 40 days, becoming less available for the bird species (Perrins, 1991). Winter moths are one of the key food items in the diet of blue tits (Evans et al., 2024). This causes blue tits and great tits to time laying date, incubation and nestling time to feed the maximum amount of nutrients to

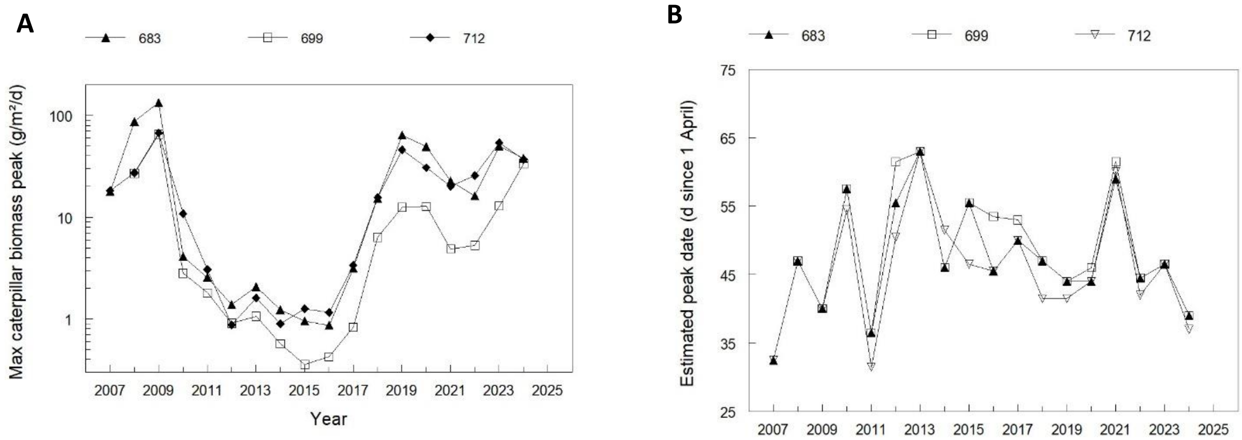


Fig. 1. Maximum caterpillar biomass peak (A) and the estimated peak date (B) in 3 trees during 2007-2024 in Nationaal Park Dwingelderveld in Drenthe

Great and blue tits live in the same habitat and feed primarily on similar prey, which may cause competition between the species (Dhondt, 2023). There are also several differences between the species for example a blue tit is only 11 g whereas a great tit is around 18 g (Tinbergen and Boerlijst, 1990; Woodburn and Perrins, 1997). The clutch size also differs with great tits laying on average 6 to 11 eggs in its nest whereas blue tits have 10 to 13 eggs (Gibb, 1950). Laying date differs between area and species, within urban areas great tits start laying earlier whereas in woods blue tits have the first eggs (Dhondt et al., 1984).

Niche theory predicts species should specialise in different resources (Ashby et al., 2017), and the question is whether we can see this when we compare the nestling diet. Furthermore, there may be a relationship between diet differentiation and resource availability, with reduced food density placing more pressure on diet differentiation. This leads to the following research question: How do great tits and blue tits change their nestling diet, in terms of number, type, and size of prey, in relation to the caterpillar peak date and height, and does this differ between the two species? We analysed diet photos of great tits and blue tits from six years to get information on the prey. For determining the caterpillar peak and date, frass nets were installed under three oak trees for the same amount of years.

The percentage of caterpillars has been shown to be higher at a high peak date and closer to the peak date (Both et al., 2009; Shutt et al., 2019). Due to great tits laying on average fewer eggs and in some areas having an earlier laying date, it is expected that great tits can time the caterpillar peak better and would thus have more caterpillars in their diet than blue tits (Gibb, 1950; Dhondt et al., 1984). Moreover, great tits tend to bring a higher percentage of caterpillars, whereas blue tits also bring a high percentage of other prey (Navalpotro et al., 2016). Nonetheless, in 88% of studies, caterpillars were the most

important food item within the nestling diet of blue tits and 79% within the great tit diet (Cholewa and Wesołowski, 2011). On the other hand, the caterpillar peak is determined by the abundance of the caterpillars and not the size, so that would be around the same for both species (Tinbergen et al., 2024). Additionally, all caterpillars are small at the start of the season, and they grow bigger over time, which might provide blue tits an advantage. Since few other studies have looked for a connection between nestling diet and caterpillar peak height and date, we tried to include both peak variables in our results.
To answer the research question we also had two other aims 1) What is the difference in the number of prey per trip between great tits and blue tits? 2) Is there a difference in caterpillar biomass brought in per hour per nestling? Blue tits tend to bring more prey per hour than great tits (Navalpotro et al., 2016), which might suggest that they also bring more prey per trip than great tits. However, the likelihood of multiple-prey loads is similar, great tits bring on 6.4% of their trips more than 1 prey (Naef-Daenzer et al., 2000) and blue tits have multiple-prey loads on 6.2% of their trips (García-Navas and Sanz, 2010). Overall is the prey size that blue tits bring to their nestlings smaller (Navalpotro et al., 2016), but for both species will the size likely decrease as the amount of prey in their beaks increases. Besides, blue tits are significantly smaller than great tits (Woodburn and Perrins, 1997) and therefore might be expected to bring less biomass per hour per chick, because they need less energy to grow We tested this by measuring and weighing self-caught caterpillars, measuring the beak size of great tits and blue tits and converting these lengths and weights into biomass. We used the data from the analysed photo sessions for the number of prey per trip.

Methods

Study area and species

The field observations for this study – the diet observations, determining the caterpillar peak, and other measurements on the birds – were done in a plot in Nationaal Park Dwingelderveld in Drenthe (52°8181″N, 6°43278″E), in an area of about 800 by 350 metre where the forest mainly consists of pedunculate oak (*Quercus robur*). The data used for this study was collected during several years between 2008 and 2024 (Table 1) from blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) breeding in nest boxes in this area.

Table 1
the total number of observations

Year	2008	2014	2015	2020	2023	2024
# Blue tits	2	2	2	2	2	2
# Great tits	1	2	2	2	2	2

Diet observations

The diet observation data were achieved using camera traps which were set up on the nest boxes in which blue or great tit nestlings were present. The diet observations were carried out when the nestlings were 8 to 17 days old, with most of them being between 9 and 14 days old. See Table 2 for the exact number of chicks and their age at the time of the pictures being taken. The selection of nest boxes was based on several parameters. First, we determined which years we would use, we based our selection on the height of the overall caterpillar peak in those years in Dwingelderveld. We did not base it on the peak calculated from the data of our three trees, however, whether the peak is very high or low is not specific on such a small scale, so this gave us a good approximation. In our selection, we included years with a high caterpillar peak (2008 and 2023-2024), a low caterpillar peak (2014-2015),

and a peak that is neither very high nor very low (2020). Due to these differences, we can really compare the diets against the different heights.
The nest boxes were selected based on the tree species around the nest box: they are all in parts of the forest mainly populated by Pedunculate Oaks, since in the plot there are also small areas with other proportions of trees. Having all of the nest boxes in the same area ensures that the habitat, and thus also the food availability, differ as little as possible. Due to our caterpillar measurements originating from oak trees, having an area with mainly oak trees ensures that our measurements are as similar as possible to the actual caterpillar availability. They were also selected based on the number of chicks, with all of them having a clutch size of at least five, and based on the age of the chicks at the time of the picture session, with all of them being at least eight days old. In 2024 the pictures were taken at a date at which the chicks had a similar age to those in previous years.
The pictures were taken using a Nikon D3100 camera with a Nikon 40mm f/2.8 G DX Micro-NIKKOR lens (Nicolaus et al., 2019). The camera was placed in a box behind the existing nest box, as can be seen in Figure 2. The nest box was lit up using LED lights to ensure that the prey were visible in the pictures. During setup, first, the camera box was attached to the back of the nest box, then the camera and lights were placed in, and then everything was turned on. Between each step, some time was given to the birds to see if they would accept the setup, and if they did not accept it within an hour everything was removed and it was tried again another day or on another nest box.
The camera was set up in such a way that a frontal picture was taken every time one of the parents came in, which allowed us to identify the prey and score their size relative to the width of the base of the beak. The pictures were taken for around three hours, and within that time between 66 and 432 items were brought in. Most of these items were prey, but this also contains some nest materials and other non-prey items. During the scoring of the prey, we also noted unrecognised prey. We did not include them in our determinations of the caterpillar biomass that was brought in, since we do not know how many of those prey were caterpillars. However, we did include them in the number of prey brought in per hour, since knowing the species composition of those unrecognised prey is not necessary, and not including them would make comparing the different nest boxes very difficult due to the differences in the amount of unrecognised prey. Pupae were not counted as caterpillars as their nutritional value differs between the first stages and last stages of pupation. If we had included pupae we also needed to have a conversion factor, while currently we only have a conversion factor for the caterpillars.

Table 2

Number of chicks and age per observation

Year	Species	Number of Chicks	Age Chicks
2008	Blue tit	11	17
2008	Blue tit	12	11
2008	Great tit	6	11
2014	Blue tit	6	14
2014	Blue tit	9	14
2014	Great tit	7	14
2014	Great tit	5	14
2015	Blue tit	6	13
2015	Blue tit	9	13
2015	Great tit	7	13
2015	Great tit	7	13

2020	Blue tit	8	9
2020	Blue tit	6	8
2020	Great tit	11	9
2020	Great tit	7	11
2023	Blue tit	10	11
2023	Blue tit	8	9
2023	Great tit	6	10
2023	Great tit	8	9
2024	Blue tit	13	11
2024	Blue tit	12	13
2024	Great tit	8	9
2024	Great tit	7	9

Fig. 2. Camera setup

Calculating caterpillar mass

In order to calculate the caterpillar mass from the relative prey size, we needed to convert the relative size to the absolute size and then find a way to convert the length to mass. For the first step, we measured the size of the base of the beak, since this is what the relative size was expressed in, of multiple individuals in our study area for both the blue tits and great tits. The measurements were taken from three blue tits and four great tits, and since there is minimal variation within the species and between sexes this should be enough to give an accurate average. Then we took the average of those sizes for both species (GT: 55 mm; BT: 45 mm) and multiplied those numbers with the scored relative size of each caterpillar. Next, we had to convert the length to mass, which we did by collecting caterpillars and weighing and measuring them. The caterpillars were collected by capturing every caterpillar we found in half an hour of looking for them in mainly Oak trees. We then weighed every caterpillar using a precision scale (precise to 0.001 g), measured their length (precise to 1 mm) and noted which species (or if not known, which family) they were. Then using a nonlinear least squared model in R we calculated the mass from the length of the caterpillars (nls; t=16.83; df=208; $p=2^{-16}$). This relationship can be found in Figure 3, with a conversion factor of Weight=0.01*exp(0.11*Length). The caterpillars used for this model mostly consisted of Geometridae, Tortricidae, and Noctuidae. The model for Noctuidae follows the average model, but for Geometridae, the conversion factor is Weight=0.01*exp(0.09*Length) (nls; t=2.758; df=14; p=0.0154) and for Tortricidae it is Weight=0.01*exp(0.12*Length) (nls; t=10.05; df=154; $p=2^{-16}$). This difference shows that including more caterpillars and a bigger diversity of families could have led to a slightly different conversion factor.

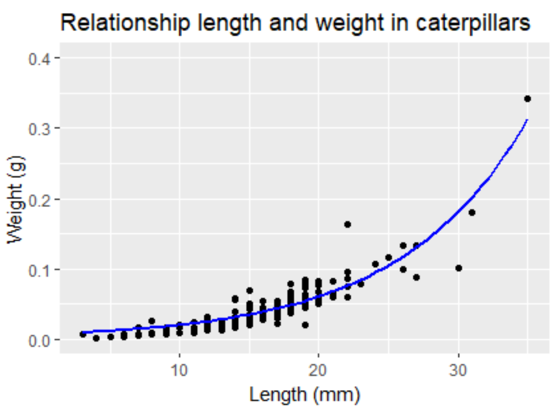


Fig. 3. Exponential line of length (mm) and weight (g) of all self-caught caterpillars

Determining caterpillar peak date and height

In order to determine the caterpillar peak, frass nets with an area of 0.25 m^2 were installed underneath the crowns of three Oak trees within our study area. By only using nets within our study area we get a caterpillar peak date and height that are as representative of the food availability as possible. These nets were installed in the same place, so underneath the same tree, every year. The caterpillar frass was caught in these nets and they were emptied every one to four days, depending on estimations of how close it was to the caterpillar peak and on rain predictions, in order to avoid wet samples since they are much harder to sort and analyse. After collection, the frass was dried in an oven (48 hrs at 60 degrees) and was subsequently sorted using sieves, cleaned, and then weighed. This data was then converted into caterpillar biomass using a conversion factor from dry frass weight to caterpillar biomass found by Tinbergen *et al.* (2024), which was temperature dependent. The temperature correction was based on the temperature data from the KNMI station in Hoogeveen, which is located about 12 kilometres from our study area. In this way, the date of the caterpillar peak and its corresponding height expressed in biomass (g/m^2/day) can be determined.

Statistical analyses

We used R (RStudio version 4.2.2) for the graphs and statistical analyses. The packages lme4 (version 1.1-31) and lmerTest (version 3.1-3) were used for the linear model and mixed models. For the paired diet observation figures, paired t-tests were performed where one BT and one GT, from the same year whose nest boxes were located close to each other, would become a couple. This means that there are two paired observations per year, except for 2008 because there is only one GT in that year. So nest box 685 in 2008 was removed from the dataset since that BT could not be paired with a GT. With these paired tests, the variation between the couples is being analysed. When working with the percentage of caterpillars, the group assigned unrecognised was removed from the dataset, since we cannot say that all of these are not caterpillars. Since we do not know the percentage of caterpillars within the unrecognised prey, nor the size of those prey, they are also not used in calculations concerning the caterpillar biomass per chick per hour or the average caterpillar biomass. The figures of difference in load size were analysed by both linear models and mixed models. The linear models all compare the x-axis number of prey with the y-axis mean caterpillar size and the linear regression of each separate species. Whereas the mixed model includes nest box as a random effect due to some nest boxes being used in multiple years, which could affect the analysis. The mean caterpillar size was calculated over the total number of pictures per nest box for each different number of prey. Mixed models were used to analyse the figures indicating the number of prey per hour, whereby year in all cases was used as a random effect, to account for the variability between the years. For consistency, the number of prey per hour was used instead of the total number of prey, due to the session length being quite variable. Here, the unrecognised prey are included, since it does not matter which type of prey they are.

Results

Caterpillar peaks

The caterpillar peak is extremely variable. It varies both in the date at which the caterpillar biomass is at its peak, and in how much caterpillar biomass there is at that date. These variations can be seen in Figure 1 where the caterpillar peak of the last 18 years in Dwingelderveld can be seen. From these 18 years, we selected six years for our diet observations. Table 3 shows the height of the peak in those years, calculated from the data collected in just our area, instead of the whole of Dwingelderveld. It can be seen that 2014 and 2015 are both years with an extremely low peak in caterpillar biomass, whereas 2008 had a really high peak in caterpillar biomass. 2020, 2023 and 2024 have an intermediate peak in caterpillar biomass with all of those values falling between 30 and 40 g/m^2/d. Table 3 also shows the date at which the caterpillar biomass peaks. The peak was quite late in 2015, whereas it was quite early in 2024. The other years all had intermediate peak dates. When comparing the peak dates with the dates at which all of the sessions took place, there was only one blue tit pair in 2014 whose session took place before the peak, while all the other sessions took place after the peak. However, when looking at the hatching dates, there is a lot of variation between the relative dates to the caterpillar peaks. The earliest hatchlings were born approximately 16 days before the peak, and the latest ones were born around 2.5 days after the peak. This indicates that the hatching dates are not really following the peak date. The fact that most sessions took place after the peak seems to be mostly due to the sampling taking place at that time instead of the actual adjustment of the hatch date to the caterpillar peak date.

Table 3

Caterpillar peak date and height during multiple years

Year	Peak Date	Peak Height (g/m^2/d)
2008	47	47,09922333
2014	47,83333333	0,897841
2015	52,5	0,858395533
2020	44,66666667	30,97390667
2023	46,5	38,96666667
2024	38,33333333	36,11666667

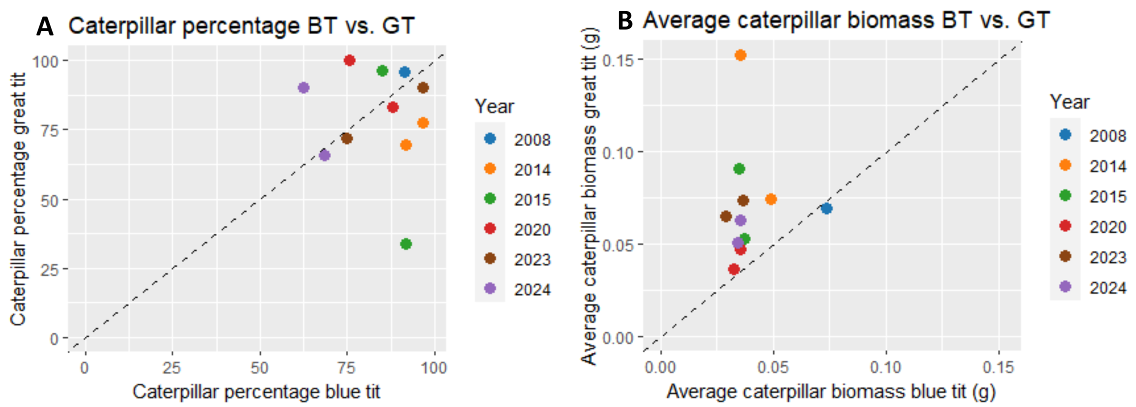
Paired diet observations

Blue and great tit diets consisted on average of 82% caterpillars, and in the paired observations we found no difference between the species (Figure 4a; Paired t-test; t=0.61896; df=10; p=0.550). The percentage of caterpillars was calculated by dividing the total number of caterpillars by the total number of prey. In all but one case, caterpillar proportions were above 65% of known prey items. In one session in 2015, Great Tits caught a lot of wasps and wasp beetles during the photo session causing the caterpillar percentage to be noticeably lower than the other couples.

Great tits brought on average larger caterpillars than blue tits at the same time (Figure 4b; Paired t-test; t=-3.1302; df=10; p=0.01069) The caterpillar biomass brought in by Blue Tits is on average between 0.025 and 0.05 g, with only the single point in 2008 being outside this range. In contrast, Great Tits varied more in average caterpillar biomass brought in between years but also within the years. In 2014 one Great Tits pair brought in a high biomass, presumably because the session was late in the season. This was the latest date in our dataset (59 April), causing most caterpillars to be pupae and the caterpillars that remain are probably bigger in size and thus have a higher biomass on average.

The chicks of great tits get fed double the biomass of caterpillars per hour compared to the chicks of blue tits (Figure 4c; Paired t-test; t=-5.3454; df=10; p=0.0003257). There is a visible difference between Figure 4b and Figure 4c, which shows that some of the differences in Figure 4b are caused by the difference in number of chicks. For instance the

2008 pair: it seemed quite out of place in terms of average biomass, but per chick it fits in very nicely with the rest of the group. This could be caused by the difference in number of chicks between that BT and GT (difference of five chicks), and the BT might have compensated for their higher number of chicks by bringing bigger caterpillars.



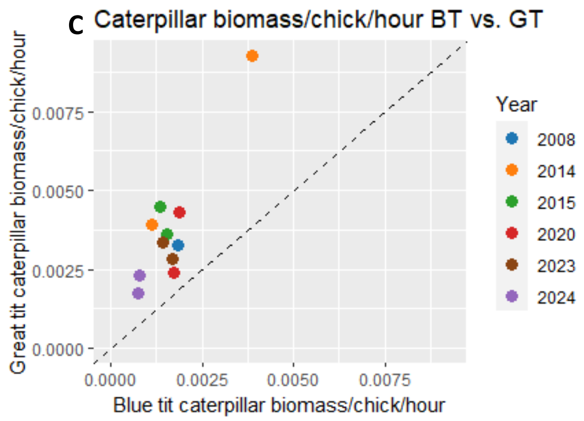


Fig. 4. Paired data of blue tits and great tits with the caterpillar percentage (%) (A), average caterpillar biomass (g) (B) and caterpillar biomass per chick per hour (g/h) (C) during multiple years.

Differences in load sizes

Our data shows that both species bring in multiple-prey loads on occasion, however, we did find a difference in how often this occurred. From our observations (Table 4) we found that 83.3% of the blue tits brought in more than one prey per trip on average, while only 54.5% of the great tits did. However, since our data includes only 12 blue tits and 11 great tits, this difference is not significant (Fisher's test; p=0.193; OR=4.167) and we would need more data to be able to say anything about the occurrence of this behaviour in blue tits and great tits. We also found that on average, in the nest boxes at which multiples were brought in (so not looking at the ones with always one per trip), there were 1.176 prey brought in by the blue tits and 1.090 by the great tits. So the blue tits that brought in multiple prey did so more often than the great tits, or they brought even more than two prey per trip. The blue tits that showed multiple-prey loading behaviour brought in, on average, 22.5 multiple-prey loads. The multiple-prey loading great tits only brought in 5.5 multiple-prey loads on average, so it seems like it is much more incidental in the great tits than in the blue tits. Out of all the instances where more than two prey were brought in, only one was a visit by a great tit, all other 24 instances were blue tits. There even was a blue tit that brought six prey during one trip.

Looking at Figure 5, the mean caterpillar size of great tits is a little more than twice as high as the size of prey blue tits feed their nestlings. However, the caterpillar size of great tits has a higher deviation than blue tits. When looking at the decrease in prey size with multiple-prey loads in blue tits there is a significant decrease with each extra prey brought in (Linear model; t=-3.567; df=1504; p=0.000373), while for great tits this is not significant (Linear model; t=-0.92; df=688; p=0.358). Both of these tests are linked to Figure 5a, not including single-prey loaders. The points on the y-axis are the average size of all the prey when having one or two prey in their beak for each nest box separately. Even when looking at just the reduction in size between a single-prey load and a double-prey load, it is not a significant reduction for great tits (Linear model; t=-0.979; df=687; p=0.328). Since one of the species does show a significant reduction and the other does not, the degree of the size reduction is significantly different for both of the birds (Mixed model; t=-2.805; df=12; p=0.011659). This model includes the number of prey in correlation with the species compared to the mean caterpillar size. The nest boxes were used as a random effect because some nest boxes were the same in different years. When doing a mixed model with nest boxes and years as a random effect the size of the caterpillars that great tits feed their young significantly differs compared to the caterpillar size of blue tits (Mixed model; t=3.414; df=12; p=0.00527). With this model, the same nest boxes in the same years are taken into account as this is more dependent. This model also includes all prey instead of a mean caterpillar prey size, whereas in the other models mean caterpillar size was used.

Table 3

Number of prey in blue tits and great tits

BT that brought multiple prey	83.3%
GT that brought multiple prey	54.5%
Average # prey BT	1.146
Average # prey GT	1.049
Average # prey BT that brought multiple prey	1.176
Average # prey GT that brought multiple prey	1.090
Average occurrence multiple prey per hour BT	7.609913
Average occurrence multiple prey per hour GT	2.015323

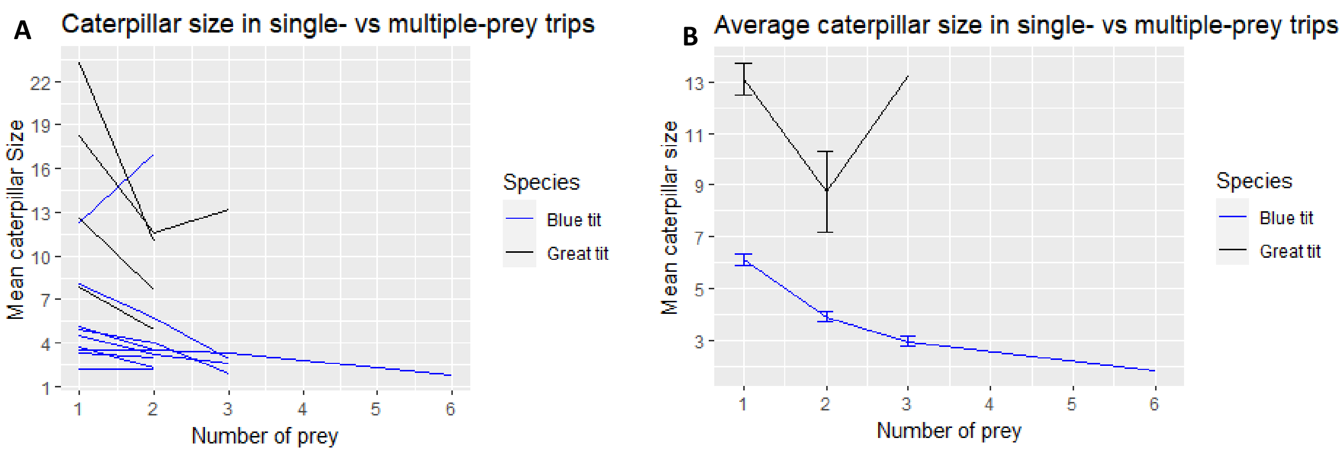


Fig. 5. Average caterpillar size in single- vs multiple-prey trips for all the nest boxes separate (A) and average of great tits and blue tits (B).

Number of prey per hour

Despite the large variation in caterpillar peak heights between years, we found no correlation between the rate of prey delivery per hour and the height of the caterpillar peak for blue tits (Mixed model; t=-1.852; df=10; p=0.093751) and great tits (Mixed model; t=-0.223; df=9; p=0.83472), however blue tits had a higher feeding rate than great tits (Mixed model; t=-4.044; df= 21; p=0.001). We included year as a random effect in these models due to the variations between years. The unrecognised prey are included in these figures because we assume the distribution of the unrecognised prey is the same as the recognised prey. There are also small differences between the figures. For the great tits, the proportion of caterpillars seems quite high in all years except for 2015, where it is much lower. This does coincide with the caterpillar peak being very low, so it seems that the great tits switched to a more varied diet in that year to correct for the lower peak. While for the blue tits, the proportion of caterpillars seems a bit more stable over the years, with it just being a bit lower in 2024. This is most probably due to the high number of pupae brought in by one of the blue tits that year.

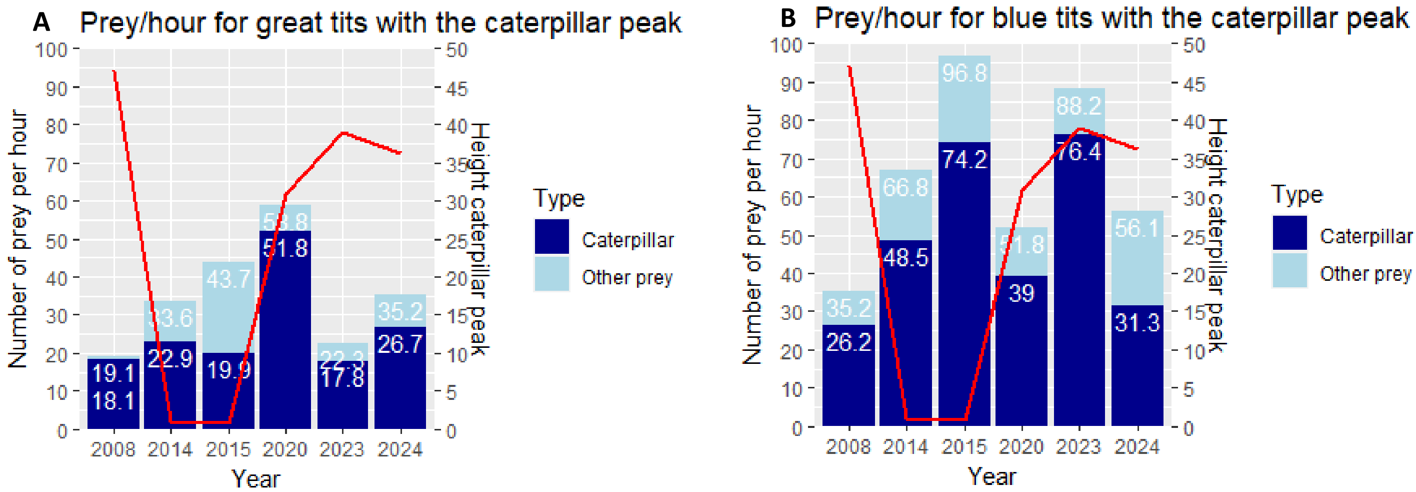


Fig. 6. Number of prey per hour combined with the caterpillar peak for great tits (A) and blue tits (B) during multiple years.

Family

The caterpillar portion of the Great Tit and Blue Tit diet consists mainly of three Lepidoptera families: Noctuidae, Geometridae and Tortricidae. For the most part, the family distribution is very similar for Blue Tits and Great Tits (Figure 7). Some noticeable differences are the number of Tortricidae and Noctuidae in 2014, 2020, and 2023, with Blue Tits having more Tortricidae and Great Tits having more Noctuidae, and in 2024 the Great Tits have a relatively high number of Drepanidae, which has not been observed in the Blue Tits in that year.

It seems that changes in the proportions of different caterpillar families in the diet are not caused directly by changes in the caterpillar peak, since there seems to be no correlation.

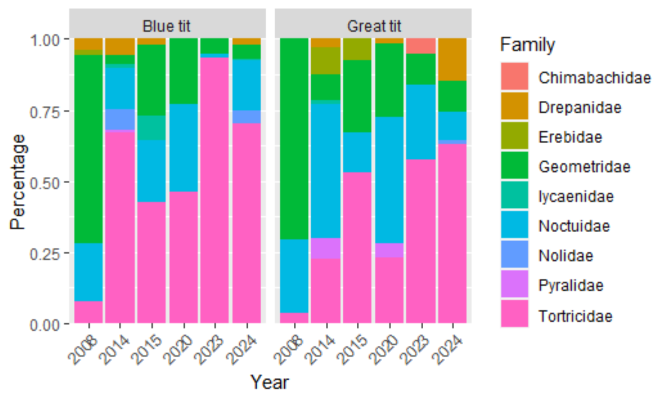


Fig. 7. Percentage (%) of different caterpillar families during multiple years

Diet compared to the caterpillar peak

We have not found any significant correlations between any of the diet variables and the height of the caterpillar peak (Table 5). Table 5 shows the caterpillar biomass and percentage, number of caterpillars per hour, biomass per hour and prey per hour compared to the caterpillar biomass at the peak. Where BT is only the data from the blue tits, GT is the data from the great tits and comparison is the peak height compared to variable*species. This gives a good view if some variables are just dependent on species and if there is a difference between the species. All these p values are extracted from linear models and the degree of freedom for the blue tits is 10, for the great tits it is 9 and for the comparison it is 19. As seen in Table 5, the correlation between the percentage of caterpillars in the diet of the blue tit and the peak height is very close to being significant, so there might actually be a correlation here. Still, more data is needed to confirm or deny that. The same goes for the biomass per hour for the blue tits and the number of prey per hour for the great tits.

Variable	BT	GT	Comparison
Caterpillar biomass	p=0.129	p=0.354	p=0.337
Caterpillar percentage	**p=0.059**	p=0.841	p=0.320
Caterpillar per hour	p=0.660	p=0.184	p=0.547
Caterpillar biomass per hour	**p=0.095**	p=0.999	p=0.429
Prey per hour	p=0.432	**p=0.084**	p=0.281

Table 5 Peak height and multiple variables

Variable	BT	GT	Comparison
Caterpillar biomass	p=0.944	p=0.786	p=0.135
Caterpillar percentage	**p=0.045**	p=0.533	p=0.612
Caterpillar per hour	**p=0.050**	p=0.386	**p=0.023**
Caterpillar biomass per hour	p=0.462	p=0.741	p=0.153
Prey per hour	p=0.141	p=0.155	**p=0.026**

Table 6 Peak date and multiple variables

Where there were no correlations between the diet variables and the peak height, there are significant correlations between some of the diet variables and the peak date (Table 6). Table 6 shows the same diet variables as Table 5, but now compared to the caterpillar biomass peak date. This was curvilinearly tested, so the date squared was used and looked at for the p-value. BT and GT are again with only blue tit data and great tit data, but in this case, the variable is compared to the date and squared date. For comparison, the variable is compared to date times species and date squared times species. All analyses are linear models and the degree of freedom for the blue tits is 10, for the great tits it is 9 and for the comparison between the two it is 19. Significant correlations are only found for the blue tits, and no correlations were found for the great tits. For blue tits, caterpillar percentage and caterpillar per hour are significantly affected by the caterpillar peak date. This can be explained by the fact that blue tits feed their nestlings twice as much as great tits. Indicating that when blue tits forage closer to the peak date they can find the caterpillars faster, and further from the peak date the birds have to spend more time looking for caterpillars. As for the comparison, blue tits and great tits vary significantly in their reaction to the relative date for both caterpillar per hour and prey per hour. This is again due to more time foraging when the species are further from the peak date.

Conclusion and Discussion

We studied the diet difference between blue tit and great tit nestlings by looking at the average caterpillar mass, caterpillar biomass, biomass per chick per hour, prey per trip, prey per hour and caterpillar families. The diet of both species consists of 82% caterpillars, but caterpillar biomass and biomass per number of chicks per hour was significantly more for great tits. The mean caterpillar size great tits feed their nestlings is twice as big as blue tits and the caterpillar size of blue tits decreases significantly with multiple-prey loads. Blue tits bring more prey per hour than great tits, but this is for both species not correlated with the caterpillar biomass peak height. The different caterpillar families are also not correlated with the caterpillar peak. So overall, blue tits bring more prey per hour and trip, and prey size is smaller compared to great tits. These differences are not correlated with the caterpillar biomass peak height, however, if more data was implemented some variables could be correlated. Conversely, caterpillar percentage and caterpillar per hour of blue tits are significantly affected by the caterpillar peak date. Moreover, both species combined vary in caterpillar per hour and prey per hour with regard to the peak date.

Caterpillar Peak & Pupae

The caterpillar peak is never too low causing the species to switch that year completely to other prey (Nadolski et al., 2021; Perrins, 1991). However, it would be interesting to study the percentage of caterpillars in the diet of second clutches of blue tits and great tits. Caterpillars are the most important food source for great tit nestlings from the second brood, according to 50% of studies, although, since most studies concentrate on the first brood, this number may be lower or higher (Cholewa and Wesołowski, 2011). After the caterpillar biomass peak, there is a large decrease in the number of caterpillars available for the bird species (Naef-Daenzer and Keller, 1999). So birds laying a second clutch need to have an early date or maybe their diet would include more other prey. That is what we saw as well in the sessions of 2024. We noticed the birds bringing a high number of pupae to their nestlings, whereas sessions shot around the caterpillar peak date these numbers were lower. However, in most studies is the winter moth the most abundant, but they pupate in the ground (Naef-Daenzer and Keller, 1999). Thus, during years with a high amount of Tortricidae, the amount of pupae in the nestling diet should also be higher. Nonetheless, we needed a bigger sample size and a smaller group of unrecognised in our data set to test this.
We found significant results regarding foraging and the caterpillar biomass peak date, but not with the peak height. Even though there is a great variability of caterpillar abundance between years (Nadolski et al., 2021) and energy requirements of the nestlings needs to be met to have reproductive success (Perrins, 1991). If our dataset was bigger, including more blue and great tit couple and more years, more variables would have become significantly correlated with the peak height and also date.

Prey per trip

In the beginning, it was said that only on 6.4% of great tits trips multiple prey would be in its beak (Naef-Daenzer et al., 2000). However, in our data, 54.5% of the great tits brought multiple prey per trip and 83.3% in the case of blue tits, but with our data set, 12 blue tits and 11 great tits, this is not significant. Nonetheless, blue tits brought even a maximum of 6 prey within one trip and great tits only had a maximum of 3 prey load. This was also significantly correlated with the prey size reduction. So, this would mean on average blue tits bring smaller prey to their nestlings. This affects the competition between blue tits and great tits because larger caterpillars would be less available (Dhondt, 1977). Not only bring blue tits smaller caterpillars to their nestlings the size of spiders and other prey is also smaller (Török and Tóth, 1999; Navalpotro et al., 2016).

Unknown & Unrecognised

While scoring the images, we saw a lot of unrecognised prey. These could be blurred photos, dark photos or we could just not see it clearly because the prey was mostly in its beak. We decided to include the unrecognised category in the total number of prey per hour, due to those images indeed being prey. However, a certain percentage of those images are caterpillars, causing the number of caterpillars per hour to be presumably lower. The unrecognised photos are not included in Figure 4c thus leading to a lower biomass per number of chicks per hour. This may also explain the differences between the years because some had a higher percentage of unrecognised photos than other years. This was our best way to handle the unrecognised because our data is stored in Microsoft Access and we encountered technical issues when trying to incorporate a formula for the prey/caterpillar ratio to transform the unknowns. Also within the families, we had a high amount of unrecognised caterpillars so we cannot explain the difference between the years and species, because if we had known the families of those caterpillars the figure might have looked completely different. Adding metagenomic barcoding to determine the caterpillar species would reduce this group significantly (Shutt et al., 2019)

Future research

For this research we collected caterpillars within half an hour for 4 times in multiple oak trees, however, this should have been done during the whole session so more caterpillars could be collected, due to different species peaking at different times (Naef-Daenzer and Keller, 1999). Besides, pupae can also be collected, weighed and measured during the caterpillar collection. Therefore the pupae can also have a converting factor and be included in the data analysis. If data scientists would collaborate with a project like this maybe code that would recognise the caterpillars from the photo session could be written so you would get immediate data. Also, adding more data so all years from 2007 till 2024 can be analysed and more couples per year would give a more precise analysis. Including blue tits and great tits who made second clutches and do photo sessions with them, could also be a way to improve this project.

References

1. Ashby, B., Watkins, E., Lourenço, J., Gupta, S., & Foster, K. R. (2017). Competing species leave many potential niches unfilled. *Nature Ecology and Evolution*, *1*(10). https://doi.org/10.1038/s41559-017-0295-3
2. Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B., & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *Journal of Animal Ecology*, *78*(1). https://doi.org/10.1111/j.1365-2656.2008.01458.x
3. Cholewa, M., & Wesołowski, T. (2011). Nestling food of European hole-nesting passerines: Do we know enough to test the adaptive hypotheses on breeding seasons? *Acta Ornithologica*, *46*(2). https://doi.org/10.3161/000164511X625874
4. Dhondt, A. A. (2023). Effects of competition and predation operating at individual and population levels: an overview of results from a long-term field experiment. *Oecologia*, *203*(3–4). https://doi.org/10.1007/s00442-023-05448-0
5. Dhondt, A. A. (1977). Interspecific competition between great and blue tit. *Nature*, *268*(5620). https://doi.org/10.1038/268521a0
6. Dhondt, A. A., Eyckerman, R., Moermans, R., & Hublé, J. (1984). Habitat and laying date of Great and Blue Tit Parus major and P. caeruleus. *Ibis*, *126*(3). https://doi.org/10.1111/j.1474-919X.1984.tb00260.x
7. Evans, L. C., Burgess, M. D., Potts, S. G., Kunin, W. E., & Oliver, T. H. (2024). Population links between an insectivorous bird and moths disentangled through national-scale monitoring data. *Ecology Letters*, *27*(1). https://doi.org/10.1111/ele.14362
8. García-Navas, V., & Sanz, J. J. (2010). Flexibility in the foraging behavior of blue tits in response to short-term manipulations of Brood Size. *Ethology*, *116*(8). https://doi.org/10.1111/j.1439-0310.2010.01788.x
9. Gibb, J. (1950). THE BREEDING BIOLOGY OF THE GREAT AND BLUE TITMICE. *Ibis*, *92*(4). https://doi.org/10.1111/j.1474-919X.1950.tb01759.x
10. Nadolski, J., Marciniak, B., Loga, B., Michalski, M., & Bańbura, J. (2021). Long-term variation in the timing and height of annual peak abundance of caterpillars in tree canopies: Some effects on a breeding songbird. *Ecological Indicators*, *121*. https://doi.org/10.1016/j.ecolind.2020.107120
11. Naef-Daenzer, B., & Keller, L. F. (1999). The foraging performance of great and blue tits (Parus major and P. caeruleus) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology*, *68*(4). https://doi.org/10.1046/j.1365-2656.1999.00318.x
12. Naef-Daenzer, L., Naef-Daenzer, B., & Nager, R. G. (2000). Prey selection and foraging performance of breeding Great Tits Parus major in relation to food availability. *Journal of Avian Biology*, *31*(2). https://doi.org/10.1034/j.1600-048X.2000.310212.x
13. Navalpotro, H., Pagani-Núñez, E., Hernández-Gómez, S., & Senar, J. C. (2016). Comparing prey composition and prey size delivered to nestlings by great tits (parus major) and blue tits (Cyanistes caeruleus) in a mediterranean sclerophyllous mixed forest. *Animal Biodiversity and Conservation*, *39*(1). https://doi.org/10.32800/abc.2016.39.0129
14. Nicolaus, M., Barrault, S. C. Y., & Both, C. (2019). Diet and provisioning rate differ predictably between dispersing and philopatric pied flycatchers. *Behavioral Ecology*, *30*(1). https://doi.org/10.1093/beheco/ary152

15. PERRINS, C. M. (1991). Tits and their caterpillar food supply. *Ibis*, *133*. https://doi.org/10.1111/j.1474-919X.1991.tb07668.x
16. Shutt, J. D., Burgess, M. D., & Phillimore, A. B. (2019). A spatial perspective on the phenological distribution of the spring woodland caterpillar peak. *American Naturalist*, *194*(5). https://doi.org/10.1086/705241
17. Tinbergen, J. M., & Boerlijst, M. C. (1990). Nestling Weight and Survival in Individual Great Tits (Parus major). *The Journal of Animal Ecology*, *59*(3). https://doi.org/10.2307/5035
18. Tinbergen, J. M., Graveland, J. M., Both, C. (2024). The importance of ambient temperature correction for estimating seasonality of caterpillar abundance through frass-fall. ARDEA
19. Török, J., & Tóth, L. (1999). Asymmetric competition between two tit species: A reciprocal removal experiment. *Journal of Animal Ecology*, *68*(2). https://doi.org/10.1046/j.1365-2656.1999.00283.x
20. Woodburn, R. J. W., & Perrins, C. M. (1997). Weight change and the body reserves of female blue tits, Parus caeruleus, during the breeding season. *Journal of Zoology*, *243*(4). https://doi.org/10.1111/j.1469-7998.1997.tb01976.x