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Original article

Caterpillar biomass depends on temperature and precipitation, but does not affect bird reproduction

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ABSTRACT

Complex changes in phenological events appear as temperatures are increasing: In deciduous forests bud burst, hatching of herbivorous caterpillars, egg laying and nestling time of birds when feeding chicks on caterpillars, may differentially shift into early season and alter synchronization. If timing of bird reproduction has to match with short periods of food availability, phenological mismatch could negatively affect reproductive success. Using a unique empirical approach along an altitudinal temperature gradient, we firstly asked whether besides temperature, also precipitation and leaf phenology interplay and affect caterpillar biomass, since impacts of rainfall on caterpillars have been largely neglected so far. Secondly, we asked whether abundance of caterpillars and thereby body mass of great tit nestlings, which are mainly fed with caterpillars, vary along the altitudinal temperature gradient. We demonstrated that next to temperature also precipitation and leaf phenology affected caterpillar biomass. In our beech forest, even along altitudes, caterpillars were available throughout the great tit breeding season but in highly variable amounts. Our findings revealed that although timing of leaf phenology and great tit breeding season were delayed with decreasing temperature, caterpillars occurred synchronously and were not delayed according to altitude. However, altitude negatively affected caterpillar biomass, but body mass of fledglings at high altitude sites was not affected by lower amounts of caterpillar biomass. This might be partially outweighed by larger territory sizes in great tits.

1. Introduction

During the last decades it has been shown that rising temperatures affect timing of natural events (Gordo and Sanz, 2005; Parmesan and Yohe, 2003; Root et al., 2003; Roth et al., 2014; Walther et al., 2002). Long-time studies investigating the timing of plants' leaf phenology (Schaber and Badeck, 2005) and insects' (Van Asch et al., 2013) or birds' reproduction (Both et al., 2004) found markedly shifts into earlier season; but not all species seem to shift their phenology to the same extent (see review of Visser and Both, 2005). Shifts in timing also appear according to temperature changes along altitudinal gradients in plants' leaf phenology (Schieber et al., 2013), insects' activity patterns (Illán et al., 2012) and birds' breeding behavior (Martin et al., 2009). Thus, these shifts lead to later seasons in colder, higher altitudes.

In recent years, Europe-wide studies on the effect of climate change on bird reproduction focused on timing of reproduction in insectivorous birds and their prey. These studies showed that with increasing temperature caterpillars and nestlings of great, coal, willow and blue tits (*Parus major, Periparus ater, Poecile montanus, Cyanistes caeruleus*) enhanced hatching. In addition, caterpillars occurred only during a short annual peak; consequently, insectivorous birds had to match timing of breeding season with the short seasonal availability of caterpillars (Bauer et al., 2010; Both et al., 2009; Cresswell and McCleery, 2003; Vatka et al., 2011, 2014; Visser et al., 2006; Zandt et al., 1990). If avian timing of reproduction was either too early or too late, hatching of nestlings did not coincide with the caterpillar peak and a low amount of caterpillar biomass during nestling period negatively affected nestling body mass (Buse et al., 1999; Henrich-Gebhard, 1990; Naef-Daenzer and Keller, 1999; Vatka et al., 2011; Visser et al., 2006).

Development and survival of caterpillars is ruled by temperature (Buse et al., 1999; Schieber et al., 2013), but is also indirectly affected by the development of tree foliage which they feed on (Buse et al., 1999; Buse and Good, 1996). Developmental growth of caterpillars (e.g. winter moth *Operophtera brumata*) is positively

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affected by ambient temperature (Perrins, 1991) and slow developmental growth in pine processionary moth *Thaumetopoea pityocampa* is associated with lower final larval mass (Pimentel et al., 2011). Moreover at high altitudes e.g., mortality of caterpillars increases due to colder environments, thus caterpillar abundance is lower (Battisti et al., 2005). Besides temperature, precipitation may affect caterpillar abundance (Tamburini et al., 2013), but the joint effect of rainfall and temperature on caterpillar biomass in forests has been largely neglected in current research (but see Battisti et al. (2005) and Pimentel et al. (2011)). In addition, caterpillars in deciduous forests have to synchronize their hatching to the early development of young leaves (Battisti, 2010; Van Asch and Visser, 2007), because leaves gain toughness and tannin content during season, both inhibiting the growth of caterpillars (Feeny, 1970).

Until now, it has not yet been comprehensively investigated, how the different environmental conditions such as precipitation (besides temperature) and leaf phenology interplay and affect caterpillar abundance and its phenology. Due to the complexity of weather effects on food webs over time, we investigated the impact of changing environmental conditions on selected plants, insects and birds along an altitudinal gradient as spatial analogues for climate warming effects. Since temperature decreases with increasing altitude (Rolland, 2003), a mountainous study site provides a gradually changing thermal environment, which may reflect the temperature changes noticeable during the last decades. Thus, a simple biological climate monitoring system can be easily built.

We studied a nest box breeding population of great tits in a beech forest along an altitudinal temperature gradient to investigate two research aims: A) the potential of temperature, precipitation and leaf phenology to affect caterpillar abundance and B) the effect of caterpillar biomass on reproductive success in great tits at different altitudes. Within research aim A, we assumed, first, that leaf phenology is delayed along the altitudinal gradient and second, that biomass of caterpillars, which feed on leaves, is influenced by temperature, precipitation and leaf phenology. Third, we expected that caterpillar biomass is reduced with increasing altitude. Fourth, in line with other studies in deciduous forests, we assume that in our beech forest caterpillars occur in high abundance only during a short period. Fifth, we assume that timing of these caterpillar peaks is delayed at high altitude sites, where ambient temperature is lower than at low altitude sites. Within research aim B, we assumed, first, that great tits adapt clutch initiation date to synchronize hatching date of their nestlings with the caterpillar peak. Second, we expect that a reduced caterpillar biomass at high altitude sites negatively affects reproductive success of great tits, since caterpillars are one of the main food items fed to nestlings (Naef-Daenzer et al., 2000; Royama, 1970; Van Noordwijk et al., 1995).

2. Materials and methods

Field work on bud burst, caterpillars and great tits was carried out in a mountainous forest located in Lower Austria (48°05′03″N, 15°55′24″E). The mixed deciduous forest was dominated by beech *Fagus sylvatica*. Nest boxes for great tits were provided within the whole study area (19.5 ha), but we split the area into three parts, representing three altitudinal ranges and assigned nest boxes to these altitudinal sites. Nest boxes at low altitudinal sites were mounted on a southern slope, whereas nest boxes at middle and high altitudinal sites were mounted on a northern slope. Following the three altitudinal sites, we collected data on leaf and caterpillar phenology every third day (see Visser et al., 2006) between 29-Apr and 22-June-2010 at low (566 m above sea level [asl]), middle (691 m asl) and high (877 m asl) altitude. Data on breeding activity of great tits were collected from 2010 to 2014. All statistical analyses were performed using R version 3.0.2 (R Development Core Team, 2008).

2.1. Leaf phenology of beech

Within the three sites mentioned above we measured leaf phenology at single trees. At each site, eight individual trees with a similar stem diameter at breast height (above 40 cm) were randomly chosen and phenological events of each tree were observed by the same observer using a binocular. The developmental stages were recorded every third day from 29-Apr-2010 until total leaf unfolding. Since different developmental stages of buds can be detected within a single tree, the percentage of these different stages were scored and a leaf phenological index (LPI: %) was calculated for the entire tree (for details see Löffler and Kätzel, 2009). Total leaf unfolding was defined as the first day a tree was scored with a LPI of 100%. We compared the date of total leaf unfolding of the three study sites using a non-parametric Kruskal-Wallis rank sum test, followed by pairwise Wilcoxon rank sum tests (Bonferroni correction).

2.2. Weather measurements

Ambient temperature (°C) was hourly measured at the three study sites using iButtons (DS1922L, Maxim Integrated, San Jose, USA, accuracy: 0.5 °C) in the year 2010. Comparisons with two weather stations located close to the study area at similar altitudinal ranges and geographical exposures (581 m asl, 855 m asl) proved that temperature data generated with iButtons were representative for the altitudinal range. One button at each site was mounted close to the sample trees (of caterpillar biomass). Temperature buttons were fixed underneath of the bottom plate of nest boxes using a mesh, and neither boxes nor iButtons were exposed to rainfall or direct solar irradiation at any daytime. We calculated the average temperature of the 72 h prior each caterpillar sampling event for the low, middle and high altitudinal sites. Hourly data on precipitation (mm) within the whole study area were obtained from a weather station close to the study site (7 km distance, provided by Zentralanstalt für Meteorologie und Geodynamik, official webpage, www.zamg.at). We calculated the sum of precipitation of the 72 h prior each caterpillar sampling event.

2.3. Phenology of caterpillars

To investigate the influence of weather conditions (temperature and precipitation) and leaf phenology on availability of caterpillars, we indirectly measured biomass of caterpillars in trees (Both et al., 2009; Verboven et al., 2001; Visser et al., 1998) by sampling fecal (frass) pellets of caterpillars every third day in the three sites from 29-Apr until 22-June-2010 (see also Visser et al., 2006). We used the eight randomly chosen trees per study site, from which we have collected leaf phenology data, to determine amount of frass produced by caterpillars in trees. Samples were also collected from periods of rainfall, and even when nets were wet. Then, we calculated the sum of frass dropping biomass (FB: mg m^{-2}) of both nets which was collected within three days prior sampling, and converted it into caterpillar biomass (see subsection 2.4, detailed information about frass sampling see supplementary material).

2.4. Calibration of caterpillar biomass from frass dropping samples

Tinbergen and Dietz (1994) and Fischbacher et al. (1998) calibrated caterpillar biomass from frass dropping samples and included a correction for temperature. We improved that calibration by including precipitation and leaf phenology that is assumed to affect caterpillar biomass. Therefore, we simultaneously sampled every third day caterpillars directly from branches of the trees where we collected caterpillar frass droppings from 2-May until 19-