

# Solar activity affects avian timing of reproduction

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**Avian timing of reproduction is strongly affected by ambient temperature. Here we show that there is an additional effect of sunspots on laying date, from five long-term population studies of great and blue tits (*Parus major* and *Cyanistes caeruleus*), demonstrating for the first time that solar activity not only has an effect on population numbers but that it also affects the timing of animal behaviour. This effect is statistically independent of ambient temperature. In years with few sunspots, birds initiate laying late while they are often early in years with many sunspots. The sunspot effect may be owing to a crucial difference between the method of temperature measurements by meteorological stations (in the shade) and the temperatures experienced by the birds. A better understanding of the impact of all the thermal components of weather on the phenology of ecosystems is essential when predicting their responses to climate change.**

**Keywords:** timing of reproduction; sunspots; birds; *Parus major*; *Cyanistes caeruleus*

## 1. INTRODUCTION

Timing of reproduction is a major component of fitness in many organisms. It has often been shown that birds start egg laying earlier in years with a warmer spring (Crick *et al.* 1997; McCleery & Perrins 1998; Dunn 2004) and that laying date has advanced over recent decades owing to climate change (Parmesan & Yohe 2003). These shifts in phenology are, together with range shifts, the most obvious ecological consequences of climate change (Parmesan 2006). The shifts in phenology can lead to directional selection for earlier laying, owing to a mismatch between food demands and food availability (Visser *et al.* 1998; Nussey *et al.* 2005) and, as a consequence of this mistiming, to population declines (Both *et al.* 2006). A better understanding of how climate, in all its aspects, affects organisms is crucial for our predictions of the effects of climate change.

Timing of reproduction is strongly affected by ambient temperatures as measured by meteorological stations. However, it remains to be shown that these are the most relevant temperatures as experienced by free living organisms. For example, it is well known that birds actively seek places in the sun during

winter (Carrascal *et al.* 2001), which may be substantially warmer than those measured in the shade (as done by meteorological stations). Solar activity, where measurements are sunspot numbers, is often correlated with population densities (Sinclair & Gosline 1997; Klvana *et al.* 2004; Selas *et al.* 2004). Sunspots influence both the Sun's luminosity and the Earth's climate (Foukal *et al.* 2006). The extent to which sunspots affect Earth's climate is still largely debated, but it is believed that an increase in sunspots can reduce the amount of energy and light distributed to the Earth (Foukal *et al.* 2006). Here, we will correlate sunspot numbers with laying dates in five Dutch long-term studies on great and blue tit (*Parus major* and *Cyanistes caeruleus*) populations, correcting for temperatures as measured by meteorological stations.

## 2. MATERIAL AND METHODS

Annual mean population laying dates have been recorded in five study populations of the Netherlands Institute of Ecology (1955–2006; 472 year–population–species combinations; table S1, electronic supplementary material). Nest-boxes were checked at least weekly, and laying dates of first clutches were calculated assuming that one egg per day is laid ( $n = 20\,357$ ). We have used these populations as independent measures for each species, but were interested in the effect of solar activity at a species level. Data on the phenology and maximum abundance of food during the chick-feeding period were collected by sampling caterpillar frass in the Hoge Veluwe area (Visser *et al.* 2006).

Daily ambient temperature (°C) was obtained from the Royal Netherlands Meteorological Institute's meteorological station in De Bilt ([www.knmi.nl](http://www.knmi.nl)). Temperature was measured 1.5 m above the ground level in naturally ventilated radiation shields (Brandsma *et al.* 2003). Daily number of sunspots was obtained from the National Geophysical Data Center ([ftp://ftp.ngdc.noaa.gov/STP/SOLAR\\_DATA](ftp://ftp.ngdc.noaa.gov/STP/SOLAR_DATA)). Daily total solar irradiance (TSI;  $\text{W m}^{-2}$ ; amount of radiant energy over all wavelengths that fall each second on one square metre outside the Earth's atmosphere) was obtained from the Physikalisch-Meteorologisches Observatorium Davos (<ftp://ftp.pmodwrc.ch/pub/data/irradiance/composite>; no data available prior to 1976; Fröhlich & Lean 2004). Daily solar radiation ( $\text{J cm}^{-2}$ ) at the ground level was obtained from the meteorological station in De Bilt (1958–2006). The mean of these variables was calculated for the period 16 March to 20 April (the period for which the laying dates correlate best with temperature (Visser *et al.* 2006)).

We fitted a general linear mixed model with mean population laying date as the response variable and as explanatory variables species and population (as discrete factors) and ambient shade temperature, sunspots and year (as continuous covariates) as well as all two-way interactions. Year (as a factor), population, species and their interactions were also included as random effects to account for the fact that all populations were exposed to the same annual abiotic variables (see Visser *et al.* 2003, for a similar approach). Only significant terms are presented. Analyses were weighted using the standard error of the laying date ( $1/(\text{s.e.})^2$ ). The degrees of freedom of the fixed effects were adjusted using Satterthwaite's procedure (Satterthwaite 1946).

## 3. RESULTS

We found that sunspot numbers and TSI were positively correlated (1976–2006;  $r_{30} = 0.85$ ,  $p < 0.001$ ). In contrast, solar radiation at the ground level ( $r_{48} = 0.24$ ,  $p = 0.10$ ) and ambient shade temperature ( $r_{51} = 0.12$ ,  $p = 0.39$ ; figure S1, electronic supplementary material) were not correlated with sunspot numbers.

Laying dates were correlated not only with spring ambient shade temperature (Visser *et al.* 2006), species and population (Visser *et al.* 2003) but also with sunspot numbers (table 1). In years with few sunspots, the birds often start egg laying late, while in years with many sunspots, they often lay early (figure 1a).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2009.0429> or via <http://rsbl.royalsocietypublishing.org>.

Table 1. Annual mean population laying dates (1955–2006) in relation to ambient temperature and sunspot numbers for two species (the great tit and the blue tit) in five Dutch populations (HV, VL, OH, LB and WB).

variable	<i>F</i> -value	<i>p</i> -value	level	estimate (s.e.)
sunspots	$F_{1,48.7} = 4.57$	0.038		1.731 (0.780)
sunspots * year	$F_{1,48.6} = 4.63$	0.036		–0.00088 (0.00039)
corrected for				
year	$F_{1,48.7} = 0.17$	0.682		
species * year	$F_{1,51.6} = 18.51$	<0.001	GT	0.048 (0.039)
			BT	–0.016 (0.015)
temperature	$F_{1,47} = 93.91$	<0.001		
population * temperature	$F_{4,12} = 4.41$	0.020	HV	–3.087 (0.356)
			VL	–2.234 (0.361)
			LB	–3.236 (0.361)
			OH	–3.545 (0.363)
			WB	–2.913 (0.393)
species * temperature	$F_{1,42.3} = 8.37$	0.006	GT	–2.913 (0.393)
			BT	–2.415 (0.171)

Apparently, in years with high solar activity, the birds can be held back (for reasons other than temperature, which we include in the model) and lay late, but in years with low solar activity, the birds are often late relative to what is expected from the effect of spring temperature. The sunspots effect on laying date has become stronger over our 52-year study period (table 1 and figure 1*b,c*; figure S2, electronic supplementary material). The same results were obtained when sunspots were replaced by TSI (table S2, electronic supplementary material).

Although we have only 15 years' data on caterpillar biomass in one of the study areas, there was a sunspot effect on the height of the biomass peak (figure 2), but no effect on the date of peak food abundance (correcting for temperature):  $p = 0.68$  for the quadratic term and  $p = 0.29$  for the linear term.

#### 4. DISCUSSION

We show for the first time that not only population densities but also seasonal timing are statistically related to sunspots (Sinclair & Gosline 1997; Klvaná *et al.* 2004; Selas *et al.* 2004). The same conclusion is drawn when the analyses are performed per species (table S3*a,b*, electronic supplementary material), showing that our finding is robust. But how would sun activity affect timing? We explore two hypotheses.

One hypothesis is that ambient temperatures as measured by the meteorological services differ from that experienced by birds (Carrascal *et al.* 2001) and that solar activity affects this difference. Although in high sunspot years more radiation enters the atmosphere (Foukal *et al.* 2006), there is no relationship between solar activity and the radiation reaching the surface. This makes it less likely that sun activity directly affects the differences between experienced temperatures and temperatures measured in the shade. However, the perception of the thermal component of weather results from the integral effects of all meteorological parameters relevant for heat exchange between the organism's body and its

environment. The animals' heat flow is affected directly by air temperature, vapour pressure, wind velocity and mean radiant temperature of the surroundings (Höppe 1999). Therefore, a genuine climate index considering the influence of all these parameters should be used to understand how climate affects organisms in a physiologically relevant way. A different climate index had been proposed, such as the physiological equivalent temperature (Höppe 1999; Matzarakis *et al.* 1999) for the biometeorological assessment of the thermal environment, and thus it remains to be studied how sunspot number or TSI may affect this thermal environment.

An alternative hypothesis to explain the effect of solar activity on avian timing is that there is an effect of solar activity on food abundance for the birds (Selas *et al.* 2004), for instance, on the abundance of food during the laying period. Potentially, a relationship between sunspots and this food abundance would be able to explain the stronger sunspot effect on laying dates over time: over the past 30 years, there has been increasing selection on early laying in great tits (Visser *et al.* 1998, 2006), and this may have led to birds having become more constrained during the laying period. In years with many insects, this constraint may be lifted. However we have no data on food availability during this period. Alternatively, sun activity may affect food abundance during chick feeding. For insectivorous birds, the abundance of arthropods at the time of maximum food requirement of their young is a crucial determinant of fitness (Lack 1968). In Norway, caterpillar abundance was negatively related to sunspots (Selas *et al.* 2004). High UV-B radiation in periods of low solar activity reduces the herbivore resistance of trees and thus increases the survival of caterpillars (Selas *et al.* 2004). In the present study, the abundance of caterpillars (Visser *et al.* 2006) is indeed negatively correlated with sunspots (figure 2). But there is, however, no effect of sun activity on the date at which caterpillar biomass peaks, and hence it is unlikely that sun activity affects avian timing via an effect on the phenology of the nestlings' food.

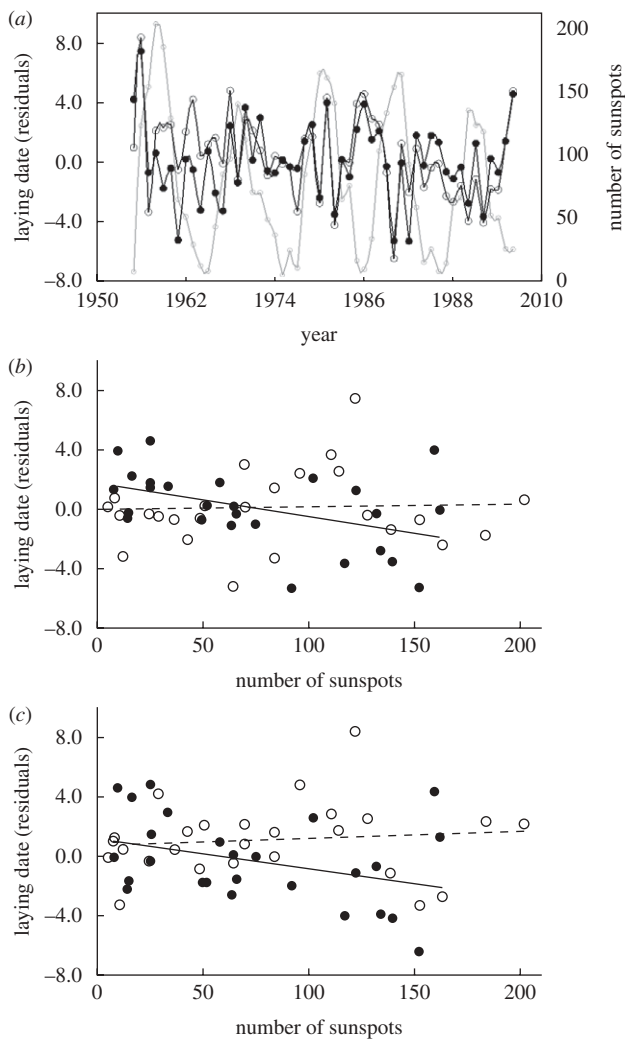


Figure 1. (a) Annual fluctuation in laying date compared with fluctuations in sunspot numbers. Laying date of (b) great and (c) blue tits versus sunspots. Because of the interaction between year (as a continuous variable) and sunspots, the data have been split solely for the purposes of illustration into those for 1955–1980 (open circle, dashed line) and for 1981–2006 (filled circle, solid line). Laying dates of both species are the residuals from the model, with population and temperature as explanatory variables.

To assess the ecological consequences of climate change, it is essential to predict the rate at which species can adapt (Visser 2008). To predict changes in timing, we need to use the ecologically most relevant temperatures. We suggest that the temperatures measured by meteorological stations may not be the most ecologically relevant. Hence, we need to take into account also other thermal components such as sunspots, radiation reaching the ground and wind speed near ground level, which affect the deviation of the temperatures as perceived by the organisms from the temperatures as reported by these meteorological stations.

We thank Jan Visser, Piet de Goede and the late Huybert van Eck for their efforts in the field and Jan Visser for careful management of the great tit data that form the basis of this paper. We thank the board of the National Park 'de Hoge Veluwe', the State Forestry Service at Vlieland and Breda

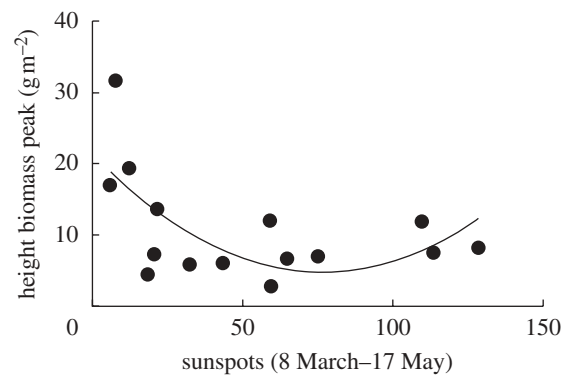


Figure 2. Data on peak caterpillar biomass for 15 years at the HV population. There is a significant negative effect of sunspot numbers (linear term:  $F_{1,12} = 7.31$ ,  $p = 0.019$ ; quadratic term:  $F_{1,12} = 5.33$ ,  $p = 0.039$ ) on biomass. There is no effect of temperature ( $F_{1,11} = 1.92$ ,  $p = 0.19$ ). Both the mean temperature and the number of sunspots were calculated for the period 8 March to 17 May (i.e. the period for which caterpillar phenology correlates best with mean temperature (Visser *et al.* 2006)).

(Liesbos), het Gelders Landschap (Warnsborn) and Barones van Boetzelaer van Oosterhout for permission to work in their woodlands for all these years. We thank the reception of the irradiance dataset (ext\_composite\_d41\_62\_0901) from PMOD/WRC. J.J.S. was supported by the project GCL2007-61395/BOS and M.E.V. by an NWO-VICI grant.

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