Influence of weather on a population of soprano pipistrelle bats in West Wales, UK: a 20 year study estimates population viability

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ABSTRACT: A nursery roost of the soprano pipstrelle bat *Pipistrellus pygmaeus* has been monitored continuously between 1 April and 27 September (Weeks 1–26) for 20 yr to promote conservation of the species, which declined over the last century. The long-term study, essential to estimate a reliable population trend, is linked to environmental changes as possible causes of decline. The main emergence was from May to July (Weeks 6–18) when 550 ± 190 (SD) *P. pygmaeus* were counted. Analysis showed that the year-to-year change in population size of female *P. pygmaeus* (ΔN) and the time of the peak exit count of the females from the roost in May to June could be predicted from the integrated air temperature (degree days, D) between 1 January and 31 March. The regression of ΔN on D showed a statistically significant linear regression line defined by $\Delta N = 1.31 - 0.0015 D$ ($R^2 = 38.4\%$; $p = 0.005$). $\Delta N = 1.04$ to 1.33 reflected a stable to increasing population (Years 1–7 and 15–20). $\Delta N = 0.78$ to 1.00 reflected a stable to decreasing population (Years 8–14). The regression of the time of the first peak exit count, calculated as the number of weeks from 1 April, on D showed a statistically significant linear regression line defined by Weeks = $12.75 - 0.020 D$ ($R^2 = 32.8\%$; $p = 0.008$). Rising temperatures between January and March would be detrimental to *P. pygmaeus* populations.

KEY WORDS: Chiroptera · Degree days · Population · Spring · Temperature · Viability

INTRODUCTION

Monitoring the conservation status of breeding colonies of *Pipistrellus* species is necessary since populations have declined since 1972 (Mitchell-Jones et al. 1999), but there are few quantitative studies of microchiropteran bats at species level to ensure good conservation practice (Hutson et al. 2001). Long-term data sets of bat populations are rare but provide estimates of the effect of climate and reproductive timing on demography of the little brown bat *Myotis lucifugus* (Frick et al. 2010). Commitment to long-term monitoring schemes is critical (Robinson et al. 2005), yet only a handful of studies have examined climate change and bats (Jones et al. 2009, Sherwin et al. 2013).

Population declines can be rapid when reproductive rates are slow (Jones et al. 2009), but bat populations are amenable to direct monitoring through nursery roost counts to assess long-term changes (Walsh et al. 2001). Half of all insectivorous bats are endangered (Racey & Entwistle 2003), and in the UK the number of pipistrelles has declined (Stebbings 1988, Walsh et al. 2001, Barlow et al. 2014). In particular, Stebbings (1988) reported that the roost counts of *Pipistrelle* spp. decreased by 62 % from 1978 to 1987. Jones et al. (2009) proposed that bat populations are declining due to environmental stresses and habitat change as a result of urbanisation, industrialisation and pollution, especially by agricultural organic matter and ammonia in water bodies.

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Bats are good mammalian bio-indicators of changes in the climate (Jones et al. 2009, Jones 2012, Sherwin et al. 2013, Russo & Jones 2015) because the rate of foetal growth can be altered according to environmental conditions (Racey 1982). Hibernation and the reproductive cycle of *P. pygmaeus* are also closely linked (Racey 1973, Racey & Swift 1981, Racey & Entwistle 2003). Hibernating insectivorous bats, such as pipistrelle species that live in north temperate zones, are susceptible to climate change because there is a narrow tolerance to variable temperatures (Foden et al. 2008). Increases in the intensity, duration and frequency of climate extremes have been predicted (Sherwin et al. 2013), and there is a broad consensus that we are currently in a period of rapid and global climate change (Hughes 2000, Parmesan & Yohe 2003). A northward shift in the range of *P. kuhlii* in eastern Europe can, at least in part, be attributed to recent increases in global temperature (Sachanowicz et al. 2006), and a temperature-dependent alteration in the range of *P. nathusii* is predicted by 2050 (Lundy et al. 2010). Thompson (1987, 1989) observed a low survival rate of pipistrelles born in 1977 and 1978, which may be attributable to ambient temperatures.

It is essential that a significant portion of an indicator species can be sampled quickly and with reasonable effort on a regular basis (Spector & Forsyth 1998), and estimations of bat populations and species trends can be made from exit counts (Harris et al. 1995). Kunz et al. (2009) define a population as a group of breeding or potentially breeding individuals of the same species present at the same time and place.

The weekly emergence counts of soprano pipistrelle bats, *P. pygmaeus*, and the daily maximum and minimum air temperatures collected for over 20 yr at Orielton Field Centre, West Wales, UK, were analysed. The main aims of this study were to determine if the year-to-year change in population size of the females, and the time of the peak exit count of the females from the roost in May to June, could be predicted from the integrated air temperature (degree days) between 1 January and 31 March. A degree day is defined as the amount of heat accumulated over a specific base temperature during a 24 h period. Degree day requirements for insect emergence have been used in pest control (Elliott et al. 2009). Adult non-biting midges *Chironomus* spp. constitute the main food items of pipistrelle bats (Swift et al. 1985, Vaughan et al. 1996, Jones & Rydell 2003). The rationale for using degree days in January to March as a predictor of the bat population parameters was that the larval development and emergence of the midges is dependent on temperature (Marziali & Rossaro 2013). The larval stage can take up to 7 wk to develop from winter to spring, when the pond mud is cold, and less than 2 wk when it is warmer (Apperson et al. 2006). The earlier emergence times of midges in warmer weather might result in lower food availability for bats later in the season. Consequently, we hypothesize that a lower number of degree days between January and March will (1) increase the year-to-year change in the *P. pygmaeus* population and (2) delay the first peak exit counts.

MATERIALS AND METHODS

Exit counts

Weekly visual counts of bats emerging from a narrow airbrick at the east end of a roof were recorded at 5 min intervals from 1984 to 1998. The time of the start, peak and end of emergence on each occasion was recorded between April 1 and September 27, Days 1–180 using the method described by Crump (1989). Weekly visual counts from 1999–2002 at the west end of the roof were made in conjunction with automated infrared beam array exit counts at the east end of the roof with similar equipment to that described by Andrews (1995). The visual counting method was verified by comparison with the automated exit counts, at the east end of the roof, stored digitally.

Environmental records

The minimum and maximum air temperature records were collected from a Stevenson Screen on site at Orielton, and daily averages were taken as the mean of these 2 values. Rainfall was also measured daily on site with a 12.75 cm diameter rain gauge (Casella).

Statistical analysis

It was necessary to make some assumptions before the data could be interpreted:

(1) There are only females in the roost (Avery et al. 1991, Webb et al. 1996);

(2) The population is loyal to the roost, and all the females return to it in May each year (Thompson 1984, 1992, Kunz et al. 2009);

(3) On average, an equal number of males and females are born (Stebbings 1968, Racey 1991, Webb et al. 1996);

(4) Only a single birth is normal, and twins do not occur (Kleiman 1969, Swift 1981, Webb et al. 1996); and either

(5.1) Females without young leave the roost before the young bats fly; or

(5.2) All the females stay in the roost until the young are flying.

The peak exit count in May–June (N_{JN}), before young are born, and the peak exit count in July (N_{JL}), after the young fly, were recorded for each year. Systematic counts in May–June (N_{JN}) and July (N_{JL}) were analysed to give the year-to-year population values. Accepting Assumptions 1 to 4 and 5.1 implies that the N_{JN} is the same as the total number of females surviving from the previous year. N_{JL} is equal to the sum of the number of young born during the summer and the number of parous females. Assumption 4 above leads to the assumption that the N_{JL} is twice the number of young. Taking Assumption 5.1 into account, Eq. (1) was used to calculate the year-to-year population (P_1) from N_{JN} and the peak counts (^{P}) in the previous year from N_{JN}^P and a quarter of the number of females that give birth in a year and the number of their young N_{JL}^P. A quarter of the females and their young in the previous year N_{JL}^P was deduced because the number of females in the roost in the previous June N_{JN}^P was equal to the number of females that gave birth. To that number of adult bats, it was necessary to add the number of female babies born in the previous July. Since half the babies were female and half male, the number of female babies was calculated as a quarter of the females and their young in the previous year. Therefore, the number of female baby bats was a quarter of the total number of bats in July in the previous year N_{JL}^P. The year-to-year population according to Assumption 5.1 (P_1), where females without young leave the roost before the young bats fly, can be calculated as follows:

$$P_1 = \frac{N_{JN}}{N_{JN}^P + \frac{1}{4} N_{JL}^P} \qquad (1)$$

If instead of Assumption 5.1 above we accept that Assumption 5.2 is correct, then the N_{JL} is taken to be the sum of the total number of females and the number of young. The corresponding values for the year-to-year population (P_2), where all females stay in the roost until the young are flying, are given by:

$$P_2 = \frac{2N_{JN}}{N_{JN}^P + N_{JL}^P} \qquad (2)$$

To investigate the relationship between the year-to-year population P_1 of *Pipistrellus pygmaeus* at Orielton and the air temperature in the spring, the

values were compared to a linear mathematical model in which their variation was represented by

$$C_y = a_0 + \sum_{m,y} a_m C_{m,y} \qquad (3)$$

where the climate value, C_y, was the value for year y, a_0 a constant and a_m the constant for a particular month m. $C_{m,y}$ are the values of the climate variable (average rainfall, average minimum temperature, average maximum temperature or mean temperature) for month m in year y. A least squares fitting procedure was used to find the values of a_m (Haber & Runyon 1979).

If it is assumed that detection probabilities remain constant through time, it is possible to obtain reasonable estimates of population change between 2 years using the ratio estimator. It was assumed that the probabilities remained constant over time and that the first peak exit counts detected the total number of females surviving from the previous year (Barker & Sauer 1995). The year-to-year change in the size of the female *P. pygmaeus* population (ΔN) was computed as follows:

$$\Delta N = \frac{N_{JN}}{N_{JN}^P} \qquad (4)$$

where N_{JN} = the first peak exit count in May to June in a year; N_{JN}^P = first peak exit count in May to June in the previous year. ΔN provided an index of the stability of the population. If $\Delta N = 1$, then the population was stable. If $\Delta N < 1$, then the population was declining, and if $\Delta N > 1$, then the population was increasing.

The *Chironomus* spp., which constitute the main food items of *P. pygmaeus*, required a certain amount of thermal time, measured in degree days, to develop. The degree days, truncated to upper and lower limits by reference to a minimum temperature threshold for midge development, were calculated using the rectangle method (McMaster & Wilhelm 1997) as follows:

$$D = \left[\frac{(T_{max} + T_{min})}{2} \right] - T_{thr} \qquad (5)$$

where D = degree days, T_{max} and T_{min} = daily maximum and minimum air temperature, respectively, and T_{thr} = the minimum temperature threshold, or a base temperature below which the midge larvae did not grow, or grew very slowly. T_{thr} was assumed to be 5°C, based on data collected on the thermal responses of the aquatic larvae of *Chironomus* spp. in European lakes and rivers where the adults emerged in spring and summer (Marziali & Rossaro 2013). The degree days at Orielton between 1983 and 2002 for

each day in January, February, and March were added to accumulate the total degree days for each year. If the calculations for any given day resulted in zero or a negative number, no degree days were added to the total (McMaster & Wilhelm 1997). Predictive linear regression models were constructed by regressing ΔN and the time of the maximum exit count on the degree days in each year between January and March from 1983 to 2002.

RESULTS

Exit counts and the values of year-to-year population size

Variations in the total number of *Pipistrellus pygmaeus* emerging during one night each week, between 1 April and 30 September from 1983 to 2002, are shown in Fig. 1 (April 1 = Day 1). Visual emergence counts made at the east end of the roost

for verification with the automated exit counts in 2000 (Week 17) and 2002 (Week 9) confirmed the same number of bats were recorded with the 2 methods, 65 and 69, respectively. The main emergence activity shown in Fig. 1 was observed between May and July (Weeks 6–18) when 550 ± 190 *Pipistrellus pygmaeus* individuals (mean ±SD) were counted. The highest count in May or June, designated the June maximum (N_{JN}), was on Week 9.1 ± 2.1, and the July maximum (N_{JL}) was on Week 15.0 ± 0.8. The values obtained using Assumptions 5.1–5.2 are listed in Table 1. The year-to-year population P_1 varied between 0.93 and 0.60 (Table 1). Values for P_1 are the ratios of the number of adult female bats in June in the current year and the number of adult bats in the roost in June in the previous year with a quarter of the number of female bats in the current year and the number of their young (Eq. 1). Values for P_2 are the ratios of twice the number of adult female bats in June in the current year and the number of bats in June and July in the previous year (Eq. 2). The re-
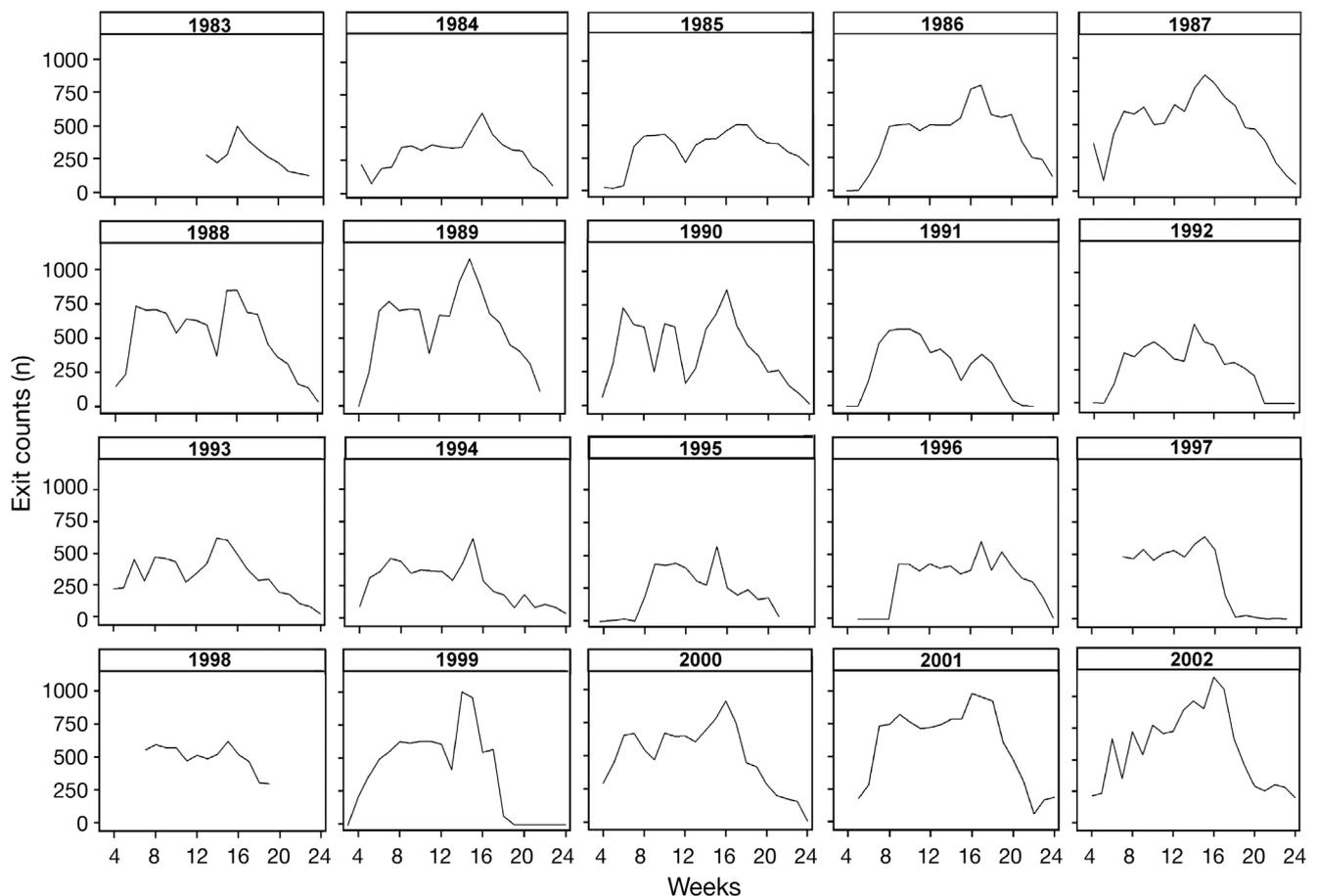

Fig. 1. Time series of exit counts of *Pipistrellus pygmaeus* from the nursery roost at Orielton, West Wales, UK, from 1983 to 2002. Week 1: week beginning 1 April. Peak exit counts in May–June are between Weeks 6 and 13, in July between Weeks 14 and 17

Table 1. Magnitude and timing of maximum exit counts (Week 1: week beginning April 1) of *Pipistrellus pygmaeus* from the maternity roost at Orielton, Pembrokeshire, UK, and the values of year-to-year population deduced from them. N_{JN}: maximum exit count in May–June; N_{JL}: maximum exit count in July; P_1 and P_2: year-to-year population calculated for Assumptions 5.1–5.2 (Eqs. 1 & 2), respectively; ΔN: year-to-year change in the size of the female population (Eq. 4); *D*: degree days (January 1 to March 31; Eq. 5). See 'Statistical analyses' for details of the calculations

Year	N_{JN}	N_{JL}	P_1	P_2	ΔN	*D*	Time of max. count (Week) June	July
1983[a]	281	500	–	–	–	142.2	13	16
1984	373	615	0.919	0.955	1.33	86.6	11	16
1985	437	550	0.830	0.885	1.17	72.1	10	16
1986	511	810	0.889	1.035	1.17	71.4	10	17
1987	656	988	0.919	0.993	1.28	71.9	12	15
1988	739	898	0.816	0.899	1.13	160.1	6	15
1989	772	1126	0.801	0.943	1.04	231.9	7	15
1990	733	868	0.696	0.772	0.95	263.8	6	16
1991	570	384	0.600	0.712	0.78	222.0	10	17
1992	474	607	0.712	0.994	0.83	185.9	10	14
1993	475	623	0.759	0.879	1.00	175.0	8	14
1994	467	621	0.740	0.851	0.98	170.9	7	15
1995	445	569	0.715	0.818	0.95	182.4	11	15
1996	430	604	0.732	0.848	0.97	112.0	12	17
1997	542	642	0.933	1.048	1.26	184.6	9	15
1998	599	622	0.853	0.971	1.11	218.8	8	15
1999	631	1006	0.836	1.054	1.05	164.8	10	14
2000	677	920	0.767	0.827	1.07	184.9	10	16
2001	825	988	0.910	0.961	1.22	80.0	9	16
2002	899	1164	0.839	1.025	1.09	99.5	13	16
Mean	576.8	755.3	0.803	0.919	1.07	154.0	9.6	15.5
± SD	162.2	223.5	0.1	0.1	0.1	59.3	2.1	0.9

[a]No data for 1982 needed to calculate P_1 and P_2 and ΔN

sults using Assumption 5.1 remained below 1.0, and the year-to-year population averaged 0.8 (Table 1). In contrast, the values for the year-to-year population P_2 were always high, mostly exceeding 0.8, and in some years exceeded 1.0, which is unlikely since these values would only occur if individual bats survived more than once. It was concluded that Assumption 5.1 was more likely to be correct than 5.2 (Table 1). Therefore, Assumption 5.1 values were accepted for further calculations.

Population dependence on weather

The effect of environmental factors on the *P. pygmaeus* population between January and July each year was tested. Using the linear model (Eq. 3), no significant dependence on rainfall was found. Initial analysis showed the best fits were obtained by using the values calculated with the monthly averages of the maximum air temperatures from January to July between 1983 and 2002. Initial results showed that

the year-to-year population values were high in years when the average maximum temperatures in March were low (Tables 1 & 2). The correlation coefficient (Pearson) for the year-to-year population P_1 (Eq. 1) and the air temperature in spring (C_y, Eq. 3) was significant (r = 0.91, p = 0.000087). The mean air temperature from January to July was also plotted with the change in the female population from year to year (ΔN, Eq. 4), and the regression slopes were significant (p < 0.05) for February, March and May (R^2 = 32.4, 42.9 27.9%, respectively) (Table 3).

The time series of the exit counts from 1983 to 2002 in Fig. 1 reflected the year-to-year patterns of variability in the first peak exit counts in May to June and the second peak exit from 3 to 10 wk later in July. The earliest first peak exit count was on May 7 (Week 6) in 1990, when the degree days (*D*) value in January to March was 263.8, reflecting a warm climate, and the latest peak was over 6 wk later, on June 24 (Week 13) in 2002, when the degree days in January to March was 99.5, reflecting a cold climate (Table 1). Further analysis was made of the effect of degree days from January to March on the changes in size of the female year-to-year population (ΔN) and the date of first peak exit peak count (Table 1). The raw data used in the statistical analysis, ΔN = 1.04 to 1.33, reflected a stable to increasing population between 1984 and 1989. ΔN = 0.78 to 1.00 reflected a stable to decreasing population between 1990 and 1996. Thereafter, ΔN = 1.07 to 1.26 reflected a stable to increasing population. The regression of ΔN, the change in size of the female *P. pygmaeus* population, on degree days is presented in Fig. 2 with 95% confidence intervals. A statistically significant linear regression line defined by $\Delta N = 1.31 - 0.0015$ (R^2 = 38.4%; p = 0.005) was plotted. The regression analysis supported the hypothesis that a lower number of degree days between January and March should be beneficial to the year-to-year change in the *P. pygmaeus* population because ΔN was high when the degree days were low and then declined linearly with respect to an increase in degree days. The theoretical maximum ΔN = 1.31 was predicted when

Table 2. Climate values calculated using the linear model with the average maximum air temperatures measured at the *Pipistrellus pygmaeus* nursery roost at Orielton from March to June. C_y: average maximum temperature value. See 'Statistical analysis' for details of Eq. (3) used to calculate the value for C_y for each year. Constant $a_0 = 1.36$. Constants for months: March $a_m = -1.09 \times 10^{-1}$, April $a_m = -1.26 \times 10^{-2}$, May $a_m = 3.89 \times 10^{-2}$, June $a_m = -8.20 \times 10^{-4}$

Year	Avg. max. temp. (°C)				Calc. variable temp. values				Σ calc. monthly values	C_y
	Mar	Apr	May	Jun	Mar	Apr	May	Jun		
1983	9.00	10.10	12.60	18.90	−0.98	−0.13	0.49	−0.01	−0.63	0.73
1984	8.36	12.20	14.51	18.29	−0.91	−0.15	0.56	−0.02	−0.52	0.84
1985	8.25	11.48	14.45	15.66	−0.90	−0.14	0.55	−0.01	−0.49	0.87
1986	8.24	8.52	12.70	17.65	−0.90	−0.11	0.49	−0.01	−0.53	0.83
1987	7.83	13.10	13.58	15.28	−0.85	−0.17	0.53	−0.01	−0.50	0.86
1988	9.20	11.90	15.30	18.47	−1.00	−0.15	0.60	−0.02	−0.57	0.79
1989	10.31	10.34	17.06	17.82	−1.12	−0.13	0.66	−0.01	−0.61	0.75
1990	10.89	12.15	17.08	16.11	−1.19	−0.15	0.66	−0.01	−0.69	0.67
1991	10.50	11.41	14.66	14.96	−1.14	−0.14	0.57	−0.01	−0.73	0.63
1992	10.00	11.22	16.36	18.69	−1.09	−0.14	0.64	−0.02	−0.61	0.75
1993	9.16	12.44	13.74	17.45	−1.01	−0.16	0.43	−0.01	−0.63	0.73
1994	9.85	11.04	14.17	16.14	−1.07	−0.14	0.55	−0.13	−0.67	0.69
1995	9.10	12.10	14.70	18.00	−0.99	−0.15	0.57	−0.02	−0.59	0.77
1996	8.40	11.00	13.80	17.10	−0.92	−0.14	0.54	−0.01	−0.53	0.83
1997	10.80	13.40	15.20	16.50	−1.18	−0.16	0.59	−0.01	−0.77	0.59
1998	10.50	10.80	16.70	16.20	−1.14	−0.14	0.65	−0.01	−0.64	0.72
1999	10.30	12.30	15.50	16.60	−1.12	−0.16	0.60	−0.01	−0.69	0.67
2000	11.00	11.40	15.80	17.20	−1.19	−0.14	0.61	−0.14	−0.74	0.62
2001	9.00	11.40	16.30	17.60	−0.98	−0.14	0.63	−0.01	−0.50	0.86
2002	10.90	12.70	14.60	15.50	−1.19	−0.16	0.57	−0.01	−0.79	0.57
Mean	9.58	11.55	14.94	17.01	−1.05	−0.15	0.57	−0.02	−0.62	0.74
± SD	1.04	1.12	1.33	1.19	0.11	0.01	0.06	0.04	0.09	0.09

the degree days were zero, with a decrease in Δ*N* of 0.0015 for every unit increase in degree day. The linear equation predicted that Δ*N* > 1 (i.e. the year to year population increased) when the degree days between January and March were ≤203.

The regression of the time of the first peak exit count (weeks from 1 April) on degree days (*D*) is presented in Fig. 3 with 95% confidence intervals. A statistically significant linear regression line defined by Weeks = 12.75 − 0.020 *D* (R^2 = 32.8%; p = 0.008) was fitted. The theoretical maximum time of the first peak count was predicted when the degree days were
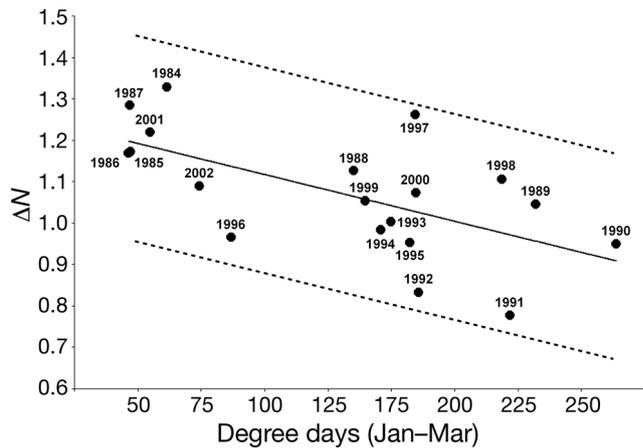

Fig. 2. Regression of year-to-year change in population size of female *Pipistrellus pygmaeus* (Δ*N*) on degree days in January to March. Dashed lines: 95% confidence intervals. See 'Statistical analysis' for details of calculations

Table 3. Linear regression ratios between the change in the size of a population of female *Pipistrellus pygmaeus* from 1984 to 2002 (calculated with Eq. 4) and the mean air temperature at the nursery roost at Orielton. Significant values in **bold**. See 'Population dependence on the weather' for details

Month	Intercept	ρ	Slope	p	R^2 (%)
Jan	1.202	<0.001	−0.023	0.286	6.7
Feb	1.296	<0.001	−0.041	**0.011**	32.4
Mar	1.682	<0.001	−0.089	**0.002**	42.9
Apr	1.476	<0.001	−0.049	0.147	12.0
May	1.933	<0.001	−0.076	**0.012**	27.9
Jun	0.829	0.205	0.018	0.703	0.9
Jul	1.244	0.034	−0.003	0.917	0.1

zero, with a decrease of 0.020 wk for every unit increase in degree day. The regression analysis supported the hypothesis that the first peak exit counts of females from the roost should occur later in June, when the number of degree days between January and March is lower, because the shortage of food in spring delays occupancy of the maternity roost, but
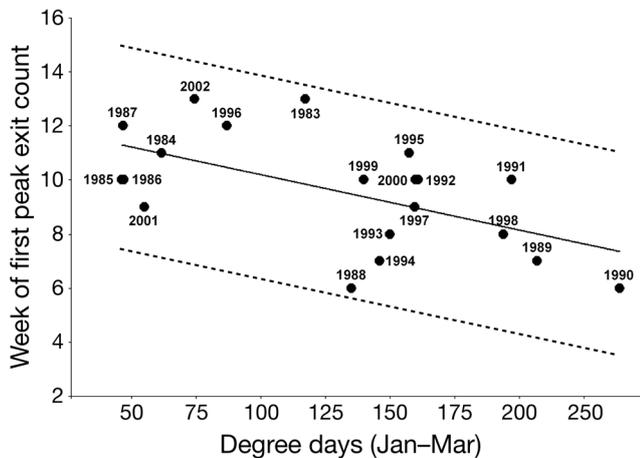
Fig. 3. Regression of time of first peak exit count in May to June of female *Pipistrellus pygmaeus* on degree days in January to March. Dashed lines: 95% prediction intervals. See 'Population dependence on the weather' for details of calculations

earlier in May, when the number of degree days between January and March is higher, because the abundance of food in spring facilitates occupancy of the maternity roost.

DISCUSSION

Dependence of the year-to-year population on low temperatures from January to March has implications with respect to climate change and the conservation of pipistrelle bats. Recent increases in global temperature are one-fifth of those expected over the next century (Sherwin et al. 2013), and climate influences bat access to food, reproduction and development (McOwat & Andrews 1995, Heideman 2000, Sherwin et al. 2013).

Effect of rising temperatures on the viability of *Pipistrellus pygmaeus* populations

This study showed that the temperature integrated over time, degree days, had an effect on the population of *P. pygmaeus.* The lower number of degree days, from January to March, increased the year-to-year change in the *P. pygmaeus* population and delayed the first exit counts from the nursery roost in May–June. Lower temperatures between January and March were beneficial to the year-to-year change in the *P. pygmaeus* population, presumably because adult non-biting midges *Chironomus* spp. are the main diet of pipistrelle bats (Swift et al. 1985, Vaughan et al. 1996, Jones & Rydell 2003), and the

larval development and emergence of the midges are temperature dependent (Butler et al. 1999, Marziali & Rossaro 2013). Adult *C. plumosus* are commonly found from April to September (Burton 1968), and the larval stage in pond mud varies by 5 wk (Apperson et al. 2006). A delay in the emergence of adult *Chironomus* spp. was beneficial because the prey abundance was in summer when female *P. pygmaeus* are in the final stages of gestation or lactation (Avery 1985, Swift et al. 1985, Maier 1992). If the temperature is high in March, insects emerge over a long period and the average density is low (Avery 1985).

In this study there were 10 wk between the peak exits of adult female *P. pygmaeus* in May–June and adult females with their young in July at the highest temperatures. Since pipistrelle bats normally fly 3 wk after they are born (Racey & Swift 1981), those 10 wk entailed a prolonged period before births occurred. If there are food shortages, pregnant pipistrelles extend gestation (Racey 1973, Racey & Swift 1981). Experimentally, the timing of pipistrelle births was altered by up to 3 mo (Racey 1972). Higher temperatures during chironomid development would cause insect abundance to peak early, so by July food would be insufficient.

In March and April insect abundance is most variable when the mean temperature is close to 7°C (Ransome 1971). Bats will fly if temperatures are above 8°C (Crump 1983–2002, Andrews & Andrews 2004) when insects are active (Swift et al. 1985), but flight is energetically demanding (Hughes et al. 1995), and if insect densities are low hunting may not be profitable. Pipistrelle bats lose significant body mass during hibernation (Racey & Swift 1981), and the period after hibernation is likely to be the time of highest mortality (Sendor & Simon 2003). Dependence of the change in year-to-year population size and timing of the peak exit counts on the degree days between January and March has implications with respect to climate change and conservation. It also supports the match–mismatch hypothesis, which posits that the role of climate on the reproductive success of a predator is manifested through its effect on the relative timing of food availability during early life stages (Durant et al. 2007).

Implications for conservation of *P. pygmaeus*

The criteria for an assessment and conservation of an indicator species specified by Spector & Forsyth (1998) are that a population should be sampled quickly with reasonable effort on a regular basis. The

method of assessment of a population of *P. pygmaeus* described in this study fulfils those criteria. The use of weekly exit counts of bats from a nursery roost during May, June and July enabled predictions of year-to-year population to be made for *P. pygmaeus* without the drawbacks of the invasive capture-mark-recapture procedures (Yalden & Morris 1975). The method used was justified because exit counts of *P. pygmaeus* at Orielton were standardised and verified. Although the mark-recapture method to estimate survival was recommended by Hallam & Federico (2009), sampling methods involving capture can be labour intensive and time-consuming (Hayes et al. 2009). The challenge of using this method of monitoring is that it is difficult, costly and suitable only for sampling small numbers of bats (O'Donnell 2009). Recapture rates are low, and maternity colonies of bats are highly sensitive to disturbance, which causes abandonment or mortality (Thompson 1989, Hallam & Federico 2009, O'Donnell 2009). The potential impact of capture and marking methods on bats is that sample populations would not be representative, and significant variability in recapture probabilities by long-term studies needs to be minimised (O'Donnell 2009).

Analysis of the UK national roost counts of *P. pygmaeus* showed a significant downward trend in population overall from 1999 to 2013 (Walsh et al. 2001). However, during the period from 1998 to 2002 the national survey showed that there was a stable to increasing population, which concurs with the findings of this study. The long-term exit counts gathered nationally from more than a hundred roosts showed fluctuations from year to year, and the findings of this study revealed the environmental factors that are relevant to the design of appropriate conservation strategies.

Although *P. pygmaeus* prey includes Nematocerean Diptera, the preference is for Chironomidae and Ceratopogonidae, whose larvae are found in stagnant or slow-moving water (Barlow 1997). *P. pygmaeus* has an advantage in that the foraging range is relatively small (Nicholls & Racey 2006b) but has limitations as a specialist (Vaughan et al. 1997, Russ & Montgomery 2002, Davidson-Watts et al. 2006) foraging mainly in riparian woodland and over water (Nicholls & Racey 2006a). Agri-environment schemes have no benefit for *P. pygmeaus* since insect abundance is relatively low (Fuentes-Montemayor et al. 2011, Park 2015). Critically important in the conservation of *P. pygmaeus* is the total area of inland water bodies (Haines-Young et al. 2000) and the length of lake edges, since these factors affect the abundance of chironomids (Russ & Montgomery 2002).

Rising temperatures due to climate change would cause a higher number of degree days between January and March, which would be detrimental to *P. pygmaeus* populations. However, the increase in the number of chironomids that emerge in a larger area could be sufficient to maintain a change in year-to-year population at a stable level of 1.04 to 1.33.

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