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Foraging time and temperature affected birth timing of *Rhinolophus ferrumequinum* and predicted year-to-year changes for 25 years in a population in West Wales, U.K.

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Movements of *Rhinolophus ferrumequinum* in and out of the nursery roost at Stackpole (West Wales, U.K.) were monitored automatically from 1994 to 2018 with simultaneous measurements of roost and external air temperatures. Pups were counted manually in June–July and mean birth dates calculated. Maximal foraging times of the population between 16:00 h and 08:00 h and temperatures at midnight showed three types of activity. These types of activity explained why warmer springs were followed by earlier birth dates. When April was warmer the number of degree days, linked to the activity of night-flying insects, was higher so the maximal foraging times were longer. Hence, mean birth dates were earlier due to faster gestation. The indirect effect of degree days on the birth date, measured by the partial regression coefficient (ß = -0.321), was weaker than the direct effect (ß = -0.628) and the mediating effect of maximal foraging time was significant ($P < 0.001$). During May–June and June–July bats foraged mainly from dusk to dawn so there was little variation in the maximal foraging times of the population, and it did not significantly mediate the effect of temperature on birth date. Birth dates were later when the external temperatures in June–July were higher (ß = 0.309), but the effect was small ($R^2 = 9.5\%$). Path analysis further revealed that longer maximal foraging times of the population in April predicted the year-to-year changes in the number of births and subsequently the number of adult females. Maximal foraging times of the population in April were a major influence on birth timing and ultimately determined whether the population grew or declined.

Key words: population, temperature, nursery roost, greater horseshoe bat monitoring, mediation, foraging, birth timing, multivariate path analysis

Introduction

Although *Rhinolophus ferrumequinum* is widespread in Europe it is considered highly threatened by human activities and habitat fragmentation and this species is listed Near Threatened in the European IUCN Red List (IUCN, 2017; Tournayre *et al.*, 2019). Good conservation of bat species requires long-term data sets for evaluation of climate change on reproductive phenology and reliable estimations of population trends (Hutson *et al.*, 2001; Frick *et al.*, 2010; Andrews *et al.*, 2016; Law, 2018; Linton and MacDonald, 2018; Locatelli *et al.*, 2019). The nursery roost study by Frick *et al*. (2010) identified negative consequences for population dynamics of *Myotis lucifugus* affected by summer drying patterns and Andrews *et al.* (2016) found that rising temperatures, especially in March, were detrimental to *Pipistrellus pygmaeus* populations. The decline in populations of *Myotis* species in the USA (Ingersoll *et al.*, 2013) and the increased use of cold mines by *Myotis* species in Sweden (Rydell *et al.*, 2019) have been found in long-term studies of hibernacula. Also, a preference for colder hibernacula by

Barbastellus barbastellus has been identified (Gottfried *et al.*, 2020; De Bruyn *et al.*, 2021) and hibernacula use in the migratory patterns of *Nyctalus noctula* across Central Europe (Lehnert *et al.*, 2018). The effects of human activity on bat populations following changes in street lighting (Rydell *et al.*, 2020) and the use of fire in forests (Law and Blakey, 2021) have been shown in long-term field studies. Declines in populations can be rapid when reproductive rates are slow (Jones *et al.*, 2009) so *R. ferrumequinum* are at risk because they have one pup at a time and reach reproductive age at two years old (Ransome, 1997*b*).

Bats are good mammalian bio-indicators of climate changes (Jones *et. al.*, 2009; Russo and Jones, 2015) because the rate of foetal growth can be altered according to environmental conditions (Racey and Swift, 1981). There is also a narrow tolerance to variable temperatures (Foden *et al.*, 2008). Increase 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 and Yohe, 2003). The date that bats leave hibernation sites and return to the roost is crucial since hibernation and the reproductive cycle are linked (Racey, 1973; Racey and Swift, 1981; Racey and Entwistle, 2003). Climate may be the most important driver of bat population change (Browning *et al.*, 2021) and the detrimental effect a rise in temperatures on European bat species, in colder regions, is predicted to cause some extinctions by the end of the century (Rebelo *et al.*, 2010). *Pipistrellus kuhlii* has shifted its range northwards and it is likely that it will lose the southern portion of Europe (Sachanowicz *et al.*, 2006; Smeraldo *et al.*, 2021). In Ireland *Nyctalus leisleri*, *Pipistrellus pipistrellus* and *P. pygmaeus* are predicted to alter their distribution (Roche *et al.*, 2020) with contraction of the range for *Myotis mystacinus* (McGowan *et al.*, 2021) and in the Carpathian Mountain region a population of *Rhinolophus euryale* is predicted to adapt its distribution (Uhrin *et al.*, 2021). Also, in North America *Lasiurus seminolus* has expanded (True *et al.*, 2021). However, in drought-risk areas of the Northern Hemisphere climatically suitable areas are predicted to shrink for half of bat species including *Rhinolophus mehelyi* (Cappelli *et al.*, 2021) but increasing aridity is a global problem because many semi-arid zones are relatively high in bat species richness (Adams and Hayes, 2021). Temperature changes are most likely to affect aerial hawking species in Europe, since they are dependent on a food supply that is highly vulnerable in both time and space (Sherwin *et al.*, 2013). Dietz *et al.* (2009) reported that *Rhinolophus* species are at high risk from climate change with *R. mehelyi* most at risk but also *R. euryale*, *R. ferrumequinum* and *R. blasii.*

It is well established that nightly foraging activity of insectivorous bats are affected by local climate weather conditions (Fenton *et al*., 1997; Erickson and West, 2002; Hood *et al*., 2002; Parsons *et al*., 2006). Foraging is affected by local climate because temperature is related to food availability (Anthony and Kunz, 1977; Hoying and Kunz, 1998; Rydell, 1989; Kunz *et al*., 2009; Allen *et al*., 2010; Frick *et al*., 2012; Eghbali and Sharifi, 2019). Provision of good landscape around maternity roosts has been identified as essential for foraging (Duvergé, 1997; Ransome, 1997*b*; Entwistle *et al*., 2001; Duvergé and Jones, 2003; Fonderflick *et al*., 2015; Froidevaux *et al*., 2017, 2019; Finch *et al*., 2020). Also, Dietz *et al*. (2013) identified core sustenance zones within 1.5 km and 3.0 km radius of nursery roosts of *R. ferrumequinum* and *Myotis emarginatus*. Although Ransome (1998) reported the influence of nursery roost conditions, such as temperature, on *R. ferrumequinum* populations a detailed study regarding foraging times, roost temperature and the mean birth date is missing from the literature.

It is established that climate influences birth timing of *R. ferrumequinum* and early births followed warm springs (Ransome and McOwat, 1994). Birth timing correlated negatively with monthly mean temperatures and depended most strongly on April temperatures (McOwat and Andrews, 1995). A rise of the mean temperature from 8°C to 10°C accelerated the mean birth date of *R. ferrumequinum* by 18 days. This effect was attributed to differences in feeding behaviour as a mean daily temperature of 10°C in April and May was sufficient for two full feeds, but at 8°C only a dusk feed was possible and below 6°C there was virtually no feeding (Ransome, 1973). Annual differences in the range of mean birth dates were observed and variation in gestational length was attributed to two phases of heterothermy, an early and late phase. It was proposed that the first phase of torpor in April–May occurred when low ambient temperatures restricted insect food supplies and most bats remained underground. The late phase was considered less significant, when increased wing loading in late pregnancy coupled with shorter nights, limited foraging times. A key radiotracking study by Jones *et al.* (1995) found that in spring *R. ferrumequinum* foraged over ancient semi deciduous woodland and over pasture in late summer. Bats more than a year old foraged 2–4 km from the day roost. Ransome (1995) reported that in summer *R. ferrumequinum* increase feeding time with increasing temperature. Differences in the duration of feeding bouts, deduced from dry faecal production by Ransome (1973), were explained by the temperature dependent mechanism of arousal (Ransome and McOwat, 1994). In addition, radio tracking of *R. ferrumequinum* identified the duration of individual's foraging times (Stebbings, 1982; Duvergé, 1997; Billington, 2000 and 2001). If there is no foraging or just one short period of foraging activity during early gestation then development is suspended, and this results in later births (Ransome, 1989).

Temperature is an important factor in determining the availability of food, and therefore in the timing of arousal. Once the temperature threshold for insect flight was reached, *R. ferrumequinum* activity increased with ambient temperature. However, Park *et al*. (2000) showed that bats with lowest reserves aroused closer to dusk and so were ready to exploit any foraging opportunities, while this was less urgent for bats in good condition. Torpor bouts varied between 0.1 and 11.8 days and the duration decreased with increasing ambient temperature. It was proposed that torpor lasted until metabolic, or water balance was achieved. Arousal at 6–10°C allows bats to feed on warm evenings in April–May and thus utilize insect supplies to accelerate pregnancy. *Rhinolophus ferrumequinum* select hibernation sites very precisely to enable arousal in that range of ambient temperatures (Ransome, 1971). After arousal, when skin temperature was 20°C, euthermic activity was longer than anticipated and it was proposed that bats remained active longer to digest food after foraging, which has implications for early gestation in April–May (Park *et al*., 2000).

Roost conditions affect growth and development indirectly by affecting the length of pregnancy and therefore birth-timing. April–May is the crucial period because it is within the *R. ferrumequinum* hibernation period and conception occurs in early April (Ransome, 1998). The maximal foraging times of population of *R. ferrumequinum* at a maternity roost is an important factor and further study was recommended to find an explanation of the influence of climate on birth timing of *R. ferrumequinum* (McOwat and Andrews, 1995). Automatic monitoring of *R. ferrumequinum* movements and environmental data was set up at Stackpole in 1994 (Andrews, 1994) and subsequent reports showed seasonal variation of bat activity during the night (Andrews, 1995–2010; Andrews and Andrews, 2016). The present study summarises the work carried out between 1994 and 2018. It was possible to use integrated modelling to estimate long-term population dynamics in small populations of *R. ferrumequinum* using limited cross-sectional and longitudinal recapture methods (Schaub *et al.*, 2007). However, this long-term study of *R. ferrumequinum* had the advantage of 25 years of cross-sectional sampling of exit counts of adults throughout the night, and the birth dates of pups each year in a relatively large population.

The nursery roost at Stackpole was saved from destruction by Stephen Evans, Nature Conservancy Council (NCC), in 1977 when he sent a ring from a dead bat to Bob Stebbings who identified it as a *R. ferrumequinum* ringed by T. P. McOwat. The bat was part of a survey throughout Pembrokeshire (R. E. Stebbings, personal communication). Prior to this there was no known/confirmed *R. ferrumequinum* nursery roost anywhere in Wales. Its discovery led to the roost being protected, designated a Site of Special Scientific Interest (SSSI), and to it being managed with the NCC. A population monitoring programme followed from 1978 (T. P. McOwat, unpublished data). The nursery roost population at Stackpole is now the second largest *R. ferrumequinum* roost in U.K. and the largest in Wales (Bat Conservation Trust, 2021). However, these bats are at the northern limit of the species and vulnerable to climate change (Walsh *et al*., 2001) and a useful parameter in determining the effect of temperature on a nursery roost population of bats is the degree day, integrated air temperature (Andrews *et al*., 2016). A degree day is defined as the amount of heat accumulated over a specific base temperature during a 24 h period (McMaster and Wilhelm, 1997).

The purpose of this study was to propose an explanation for the observed correlations between the birth dates of the pups, the year-to-year changes in the population of *R. ferrumequinum*, and the environmental factors at the Stackpole nursery roost (McOwat and Andrews, 1995). The following hypotheses were tested concerning the predictive relationships between nursery roost events, and temperature-related environmental factors: i) There were direct negative correlations between the birth dates of the pups and the environmental factors in April to July, specifically the external air temperature; the roost temperature; and/or the degree days (based on the threshold temperature at which flying insects were active); ii) The direct negative correlation between the environmental factors and the birth dates of the pups was mediated or indirectly explained by the maximal population foraging times of the adult bats; iii) The effects of environmental factors on the variance in the birth dates partially explained the variance in the year-to-year change in the population.

MATERIALS AND METHODS

Stackpole Roost and the Foraging Area

The immediate foraging area around the Stackpole nursery roost allows *R. ferrumequinum* access to broadleaf woodland with a direct connection to a large lake with wooded paths. Old mixed hedgerows connect to grassland and farmed permanent pasture within 1.5 km and grazed scrub pastureland and farmland within a 3.0 km radius. There have been few changes at Stackpole during this 25 year study since it is a Special Area of Conservation (SAC) and protected from urbanisation. The National Trust owns the land (Countryside Council for Wales, 2008) and it is managed with Natural Resources Wales.

Monitoring of Pups

We followed the same methods used by McOwat and Andrews (1995). The roost was visited at intervals after the adults had left to hunt, when pups were present from June to July each year. Pups were taken down from the apex of the roof in groups, one section of the roof at a time, and their forearm lengths were measured with vernier callipers. Clipping the tips of their claws according to a predetermined binary code identified individual pups. The code was recorded with the date, forearm length and sex. The pups were then returned to the same roof section before the adults returned. The mean birth dates were calculated from the forearm length measurements ($n = 3{,}227$; 1,617 ♂♂ and 1,610 ♀♀). The birth date of each pup was calculated using the Microsoft Excel spreadsheet (Supplementary Appendix) created according to the method used by McOwat and Andrews (1995). The mean birth date was determined annually as the date when half the total number of pups were born. Time available for monitoring became insufficient between adult exit and return as the roost population increased. Since 2014, a sample of pups of the year was measured, and all were photographed in situ with Nikon SLR D50 or D5100 digital cameras with a Nikon 18–105 lens, and a computer count made from the photographs.

Automatic Monitoring of Adult Bats

The flight of greater horseshoe bats in and out of the nursery roost was recorded continuously on a computer simultaneously with environmental data. Bats were detected by automatic monitors consisting of infrared beam arrays in the roost entrance together with computer systems installed in a room adjacent to the roost. The infrared beam array was designed and constructed as described by Andrews (1994) and placed in the exit hole 45 cm^2 in the floor of the roost. Bats emerged into the dark archway of the old stable block (Andrews and Andrews, 2016). Temperatures inside the roost were measured with LM35DZ digital sensors and outside with Dallas 1821 semiconductors (RS Components Ltd. Northants, U.K.), and recorded simultaneously with rainfall and bat activity. An ARG100 rain gauge (Environmental Measurements Ltd, North Shields, U.K.), in a garden near the nursery roost, was connected to the computer via an interface. Records were collated from the computer record for comparison with nightly foraging times (Andrews, 1995–2010) and we followed the method identified by Andrews (1994) for measuring the total foraging times. Maximal foraging times were calculated from the exit counts/h for analysis using Microsoft Excel. The maximal population foraging time (*Max ft*) each night was calculated as follows:

$$Max\ ft = (P\ e \times T\ ft) \quad (1)$$

where $P\ e$ = the percentage of bats that actually stayed out ($E\ max$) of the total number of bats ($E\ t$) that could have stayed out in the total time ($T\ ft$) that bats foraged:

$$P\ e = (E\ max\ /\ E\ t)\ 100 \quad (2)$$

($E\ max$) was calculated from the number of bats that emerged during the dusk exit (E) plus the sum of the number of bats that remained out of the roost in each subsequent hour ($B\ h$):

$$E\ max = (E + B\ h) \quad (3)$$

The total number of bats that could have emerged was calculated from the number of bats at the dusk exit (E) times the total foraging time ($T\ ft$):

$$E\ t = E \times T\ ft \quad (4)$$

Total foraging times and maximal population foraging times were also visualised in computer graphs plotted between 16:00 h and 08:00 h that were available the following morning. All data were stored on the computer used to control data acquisition and analysed remotely (Andrews, 1994).

Nightly recordings of temperature, rainfall and bat activity were collected from the beginning of April to the end of July each year ($n = 122$ nights/year). These records ($n = 3{,}050$) were downloaded for analysis from the total data set of annual nightly records assembled during 25 years monitoring.

Statistical Analysis

Peak exit counts in May–June (N_{JN}) and July (N_{JL}) were recorded. The June maximum exit count (N_{JN}) is the same as the total number of females surviving from the previous year and the July maximum exit count (N_{JL}) is equal to the sum of the number of pups born during the summer and the number of parous females. The year-to-year change in the size of the female greater horseshoe population ($\Delta\ N\ p$) was computed as follows:

$$\Delta\ N\ p = N_{JN} / N^{p}_{JN} \quad (5)$$

Where N^{p}_{JN} = first peak exit count May–June in the previous year. $\Delta\ N\ p$ provided an index of population stability.

The integrated air temperature, degree days (D), were calculated using the rectangle method (McMaster and Wilhelm, 1997) as follows:

$$D = (T_{max} - T_{min}) / 2 - T_{thr} \quad (6)$$

Where: D = degree-days, T_{max} and T_{min} = daily maximum and minimum air temperature respectively, and T_{thr} = the minimum temperature threshold, below which the insects would not fly at night. T_{thr} was assumed to be 7°C (Williams, 1961; Avery, 1985, Rydell, 1989). The degree-days for each day in April, 1994–

2018, were added to accumulate the total degree-days for each year. If a day result was zero or negative no degree-days were added to the total (McMaster and Wilhelm, 1997).

Multivariate Path Analysis

Bivariate correlation analysis was not appropriate to test the hypotheses because bivariate coefficients are spurious if the reason for the correlation between two variables is their joint correlation with one or more mediating variables (Ward, 2013). Path analysis (Preacher and Hayes, 2004; Shipley, 2016) was conducted using SmartPLS 2 software to explore the partial correlations between nursery roost events, environmental factors, and foraging times. The path diagrams represented the hypothetical models predicting the direct and/or indirect effects of temperature-related environmental factors and the foraging times in April to July on the birth dates of the pups and the year-to-year change in the population. The path diagrams in Fig. 3 depict the standardized partial regression coefficients or ß weights (symbolized by arrows) between the empirical variables (symbolized as rectangles).

The mean value of a path coefficient (β) was assumed to be significantly different from zero if $P < 0.05$ for the two-tailed t-test statistic (where $t = \beta/SE$). The coefficient of determination (R^2) measuring the proportion of the variance explained was taken as the effect size. Statistics were estimated using the bootstrapping resampling technique with 5,000 random samples drawn with replacement from the data set. Bootstrapping compensates for the distortions in the empirical data caused by nonrandom sampling (Manly *et al*., 2020). The path analysis included testing for mediation, defined as the effects of a third variable that intervenes to indirectly explain the direct correlation between a predictor and an outcome (Preacher and Hayes, 2004). Model A (Fig. 3) depicts the direct effect of a predictor on an outcome in the absence of a moderator ($ß_1$) and the indirect effect in the presence of a moderator ($ß_4$). The predictor initially influences the moderator ($ß_2$), which in turn, influences the outcome ($ß_3$). The indirect effect of the predictor on the outcome ($ß_4$) is reduced compared to the direct effect ($ß_1$). If β_4 is zero, then mediation is complete, because 100% of the variance in the outcome has been explained by the mediator. If β_4 is significantly different from zero, then mediation is partial, because the mediating effect does not explain 100% of the variance in the outcome. Sobel's test was performed to compute the Z statistic which determined if a hypothesized mediator caused a statistically significant ($P < 0.05$) reduction in β_4 relative to β_1 (Sobel, 1986). All the variables were logarithmically ($\log_{10}$) transformed prior to the analysis in order to satisfy the theoretical assumptions of residual normality, linearity, and homoscedasticity (Shipley, 2016).

RESULTS

Nursery Roost Population and Births

Exit counts (Fig. 1 and Table 1), showed an annual increase in the nursery roost population 1994–2018 (Pearson, $r = 0.987$, $P = 0.001$). The first peak in the roost population (N_{JN}) was in May–June (66.9 ± 14.3 days) and second peak (N_{JL}) in July (111.8 ± 8.7 days) occurred mainly after the annual mean birth date, indicating females joined the nursery roost to give birth. The mean birth date was 8 July (99.3 ± 8.2 days) and births ranged from day 84–118 (April 1st = day 1).

Variations in Adult R. ferrumequinum *Activity*

Typical variability of *R. ferrumequinum* exit counts, the number of bats out of the roost until dawn and foraging times are shown in Fig. 2A–2D. The types of bat activity (Types 1–3) were designated according to the changes in the maximal population foraging times from April to July and the timing of the first and second peaks in exit counts in May–June and July (Table 2). The maximal population foraging times provides clear information about when no bats forage, and when only a short dusk bout occurs in April.

In April bats started to form the maternity roost population (Fig. 1) and from April to May the population increased but there were notable fluctuations in the nightly counts when bats joined and left the maternity roost population (Fig. 2A–2B). During May and June, the number of bats in the population fluctuated less and increased up to the first peak in the exit count (N_{JN}) but after the first peak the population decreased slightly. This decrease in the population could be caused by non-breeding females and/or sub adult bats leaving the roost. In June and July, the population increased again up to the second peak exit count (N_{JL}) when births occurred (Figs. 1 and 2C–2D, and Table 1). This second peak increase in the population is likely to be caused by pregnant bats arriving from the adjacent nursery roost at Slebech or elsewhere to give birth at Stackpole since the number of exit counts is often higher than the first peak (Table 1).

Differences in total foraging times (*T ft*) were dependent on day length and environmental temperature. In April, when bats started to join the maternity roost from their hibernation sites, the maximal population foraging time (*Max ft*) was relatively short (3.4 ± 1.2 h/night) because bats began their return within 30 minutes of emergence and by midnight the majority had returned (Table 2, Type 1a activity). The period for statistical analysis varied since the date when bats arrived at the maternity roost ranged from day 7 (April 7) to day 28 (April 28). The average arrival was on day 12 ± 8.2 (April 12). When the environmental temperature at midnight (*T ext*) was below 8.4 ± 1.6°C the maximal population foraging time (*Max ft*) was shorter than 3.4 ± 1.2 h/night. Therefore, the temperatures at midnight were

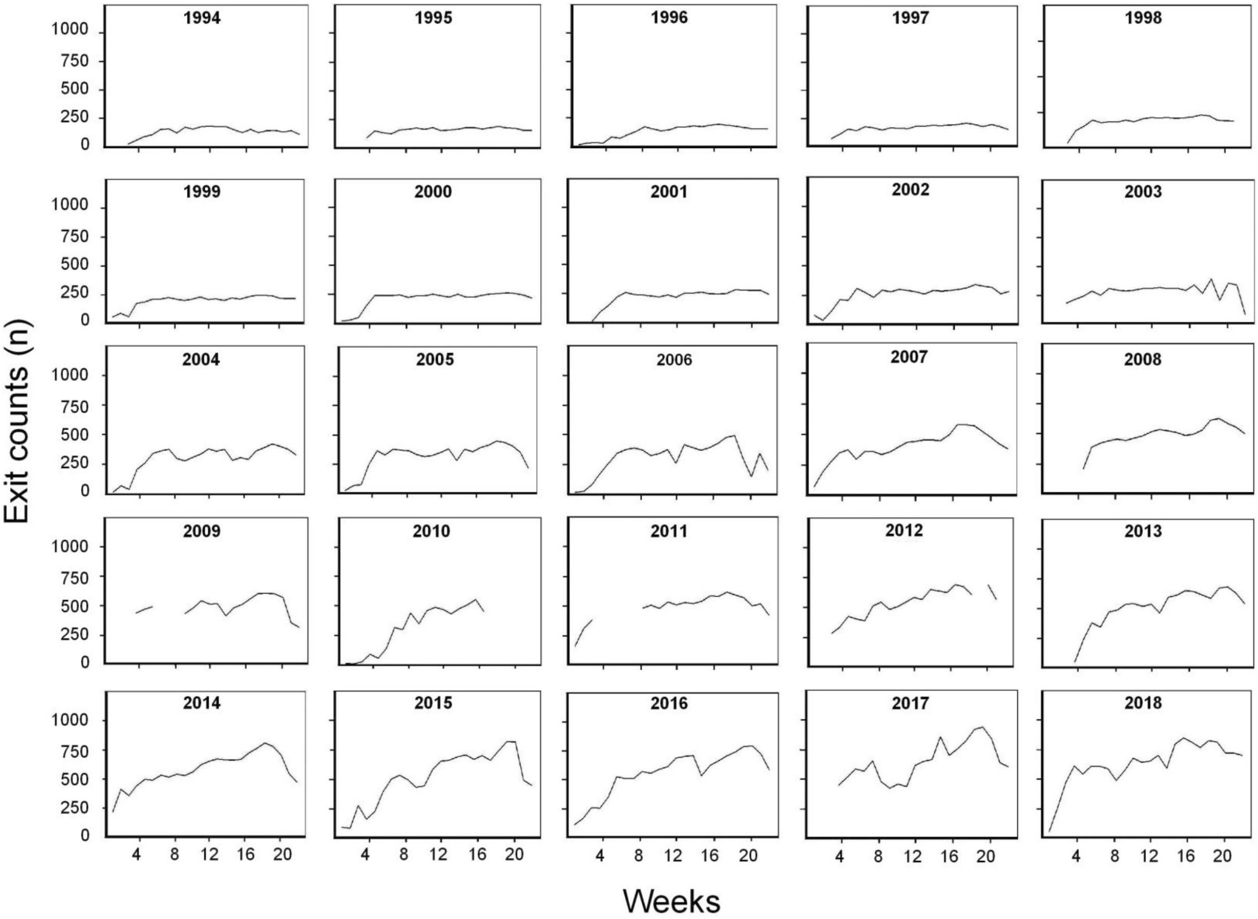

FIG. 1. Time series of exit counts of *R. ferrumequinum* from the nursery roost at Stackpole, West Wales, U.K. from 1994 to 2018. Week 1: beginning 1 April. Peak exit counts in May–June between Weeks 5 and 12, in July between Weeks 14 and 18

crucial to bat activity (Fig. 2A and Table 2). From April to May the maximal population foraging time (*Max ft* ^{1}) was longer (4.1 ± 1.1 h/night) with a small emergence after midnight and a gradual return (Fig. 2B and Table 2, Type 1b activity) and ranged from day 29 (April 29) to day 48 (May 18).

During May and June, the maximal population foraging time (*Max ft* ^{2}) was longer (5.8 ± 0.6 h/night). Bats emerged rapidly and the majority remained out until dawn. Activity culminated at the first peak in the exit count (N_{JN}) of the roost population (Fig. 2C and Table 2, Type 2 activity). The period prior to first peak in the exit count (N_{JN}) was selected for statistical analysis, deduced from the results; day 49 (May 19) to day 89 (June 29). Timing of first peak in the exit count varied annually (Table 1 and Fig. 1).

In June and July, the maximal population foraging time (*Max ft* ^{3}) was similar to May–June (5.7 ± 0.3 h/night), but typically displayed a characteristic first return to the roost around midnight and a second emergence, when mothers fed their pups during the night, before returning at dawn (Fig. 2D and Table 2, Type 3 activity). Analysis of the factors affecting the birth date, such as the maximal population foraging time (*Max ft* ^{3}), required standardization of the data as the mean birth date and the range of dates when births occurred varied annually from 1994 to 2013 (Table 1). A period of 29 days was selected for statistical analysis of the factors affecting the mean birth date each year i.e.,14 days before and 14 days after the annual mean birth date added to annual mean birth date. This period of analysis of Type 3 activity occurred around the time of the second peak in the exit count (N_{JL}) and the average period ranged from day 85 (June 24) to day 113 (July 23).

Multivariate Analysis

Data collected in April (Type 1a activity) indicated that the effects of external temperature and degree days were statistically significant (Fig. 3, Model C; Fig. 4, Matrix A; and Table 3A). Birth dates were earlier when the external temperature

TABLE 1. *Rhinolophus ferrumequinum* births, peak exit counts and integrated temperature at the Stackpole nursery roost in Pembrokeshire, West Wales, U.K.

Year	Births (n)	$\Delta N b$	Births		D	Peak exit counts		$\Delta N p$	Peak exit timing	
			Range	$\bar{x}$		N_{JN}	N_{JL}		N_{JN}	N_{JL}
1994	64		94–123	109	41.0	200	228		67	102
1995	66	1.03	85–111	97	55.6	201	199	1.01	65	109
1996	62	0.94	104–131	118	42.4	190	207	0.95	60	118
1997	69	1.11	77–112	90	80.8	195	198	1.03	74	118
1998	73	1.06	86–116	99	40.3	228	232	1.17	36	103
1999	89	1.22	85–107	92	81.7	251	243	1.10	53	117
2000	101	1.13	90–116	98	39.9	276	269	1.10	81	102
2001	115	1.14	95–125	107	38.7	297	275	1.08	49	109
2002	130	1.13	88–119	99	69.5	330	312	1.11	77	99
2003	138	1.06	86–113	96	116.5	332	333	1.01	57	120
2004	173	1.25	89–122	101	80.6	406	405	1.22	51	94
2005	175	1.01	75–114	98	110.5	395	407	0.97	56	98
2006	200	1.14	89–115	100	63.2	434	447	1.10	51	101
2007	216	1.08	74– 98	86	122.4	463	483	1.07	82	121
2008	229	1.06	95–124	105	74.2	518	547	1.12	88	122
2009	260	1.14	80–111	92	114.9	533	538	1.03	79	121
2010	253	0.97	87–127	100	105.3	520	620	0.98	60	107
2011	233	0.92	72– 98	84	152.0	525	613	1.01	68	119
2012	266	1.14	84–122	98	76.8	603	666	1.15	89	120
2013	298	1.12	100–136	109	52.8	613	639	1.02	73	116
2014	295	0.99	–	98[a]	122.0	637	692	1.04	49	119
2015	303	1.03	–	105[a]	57.7	602	715	0.95	89	110
2016	337	1.11	–	115[a]	45.1	605	742	1.00	76	120
2017	356	1.06	–	89[a]	46.4	653	717	1.08	70	113
2018	415	1.17	–	95[a]	76.3	742	786	1.14	73	117
Mean	196.6	1.08	86.8–117.0	99.2	76.3	430.0	460.5	1.06	66.9	111.8
SD	104.0	0.10	8.5–9.8	8.3	32.3	171.3	201.7	0.1?	14.3	8.7

Explanations: Births (mean) — Mean birth date (day number), when half the total number of pups were born; [a] — Mean birth dates calculated from photographic records with a sample of birth dates deduced from forearm length measurements; $\Delta N b$ — Year to year difference in the number of births; Births (range) — Start and end dates of births (day numbers). D — Degree days, integrated air temperature in April, threshold 7°C, April 1st — day 1. N_{JN} — Maximum exit count in May–June, N_{JL} — Maximum exit count in July. $\Delta N p$ — Year to year change in the size of the female population. Peak exit timing — Day number on which N_{JN} or N_{JL} occurred (Day numbers, April 1 = day 1)

was warmer. A longer number of degree days in April was the strongest predictor of an earlier birth date, indicated by the largest effect size ($R^2 = 29.6\%$, $P = 0.001$). All but one of the path coefficients were statistically significant and mediation was reflected by a reduction in the effect of degree days on the birth dates. Sobel's test indicated that the effect of mediation was statistically significant. A substantial proportion of the variance in birth date was explained by the model ($R^2 = 64.1\%$).

Log_{10} transformations were conducted to normalize and linearize the relationships between the birth dates and the environmental factors, in order to satisfy the parametric assumptions of the path analysis. The distribution patterns of the points around the regression lines in Fig. 4 reflect deviations from linearity after about 100 days. When the birth dates were later, the relationship between the birth timing and the environmental factors was not the same as when the birth dates were earlier.

Minimal foraging was observed when less then five bats emerged during heavy rainfall of 5 mm or more during the night in April (Type 1a activity). There were only seven nights in the total of 750 sampled (0.9%) when the adult bats were not able to forage due to heavy rain. During light rain, the bats continued to forage so the maximal population foraging time (*Max ft*) incorporated any effect of rain. The nights when there was heavy rain the external temperature was colder (6.8 ± 3.3°C) than the average for April (8.4 ± 1.6°C) although the roost temperatures were approximately the same (11.9 ± 3.1°C and 11.7 ± 2.2°C, respectively).

In April–May (Type 1b activity) birth dates were later when the external temperature at midnight was warmer, and when the roost temperature was cooler, but the effect sizes were small ($R^2 \leq 6\%$ — Fig. 3, Model D; Fig. 4, Matrix B and Table 3B). The effect of external temperature on birth date was mediated completely by the maximal population

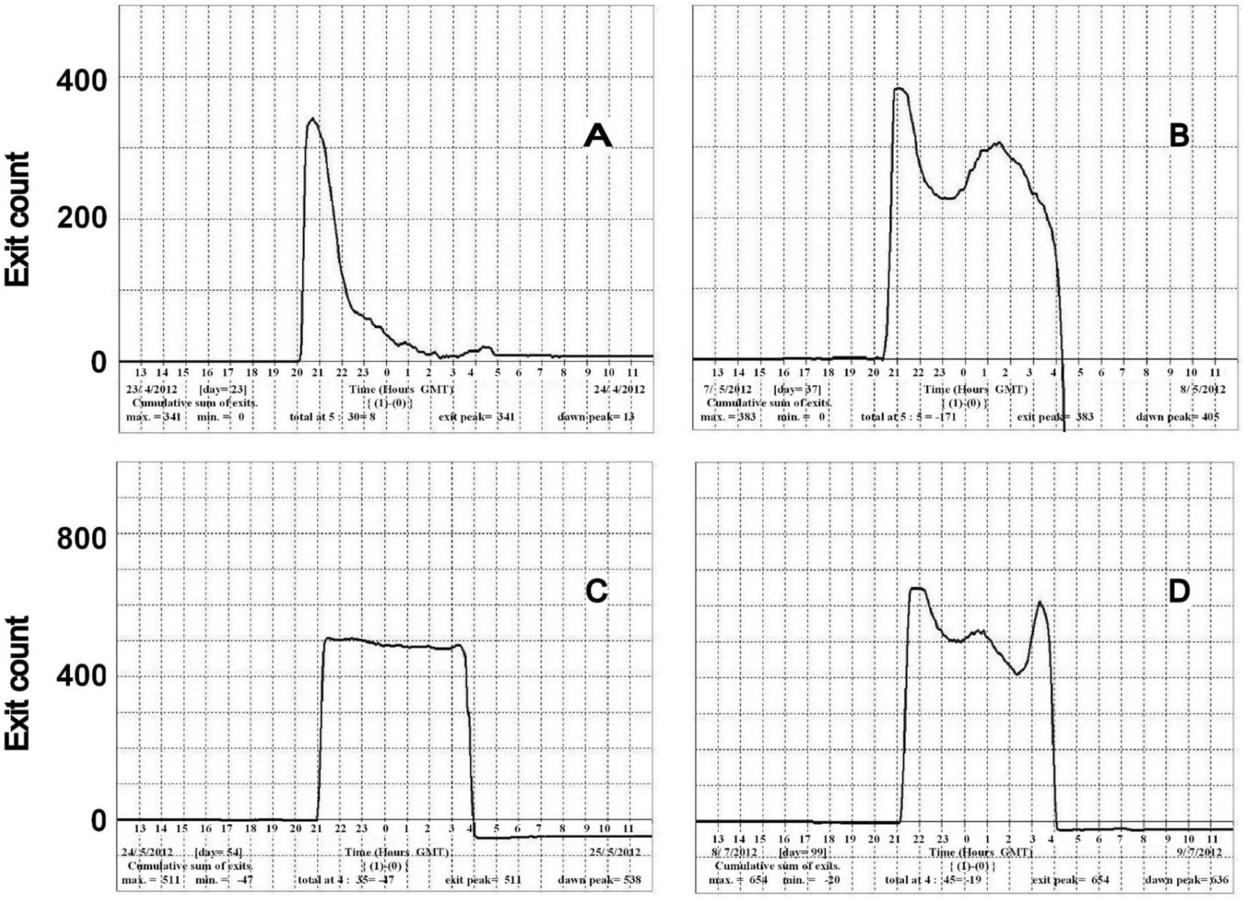

FIG. 2. Variation in exit counts and foraging times of *R. ferrumequinum* at Stackpole from April to July showing different types of activity, Types 1–3. A — Type 1a; B — Type 1b; C — Type 2; D — Type 3

foraging time. However, because less than 100% of the variance in birth date was explained, unobserved factors contributed to the variance in the birth date.

Data analysed from May to June (Type 2 activity) showed that only a small proportion of the variance in birth date was explained by the model (R^2 = 15.4% — Fig. 3, Model E; Fig. 4, Matrix C; and Table 3D). The model explained a small proportion of the variance and other unobserved factors contributed to the variance in the birth date. In June and July (Type 3 activity) Sobel's test indicated that the effect of mediation was not statistically significant (Fig. 3, Model F; Fig. 4, Matrix D; and Table 3D). Maximal foraging time in June–July did not mediate the relationship between external temperature and birth date.

Longer maximal foraging times explained why warmer springs were followed by earlier births and predicted year-to-year changes (Fig. 3, Model B). All the path coefficients were statistically significant (Table 3E). However, environmental factors and foraging times in the spring did not explain 100% of the variance in the birth date (R^2 = 54.5%).

DISCUSSION

This study confirmed findings by Ransome and McOwat (1994) and McOwat and Andrews (1995) that birth dates of *R. ferrumequinum* pups depended on environmental temperature in April but has also identified the multivariate path involved. The integrated air temperature in April, degree days, was the most important predictor of birth timing but longer maximal foraging times also explained why warmer springs were followed by earlier births and predicted year-to-year changes. The benefit of early births of *Eptesicus fuscus* proposed by Barclay (2012) was a longer growing season although geographical variations in environment would affect the length of the growing season and therefore survival.

Earlier births occurred when the number of days when air temperatures in April was above 7°C was

TABLE 2. *Rhinolophus ferrumequinum* foraging times and temperatures from April to July at the nursery roost at Stackpole, West Wales, U.K.

Year	April_(Type 1a activity)				April to May (Type 1b activity)				May to June (Type 2 activity)				June to July (Type 3 activity)			
	T ft	*Max ft*	*T ext*	*T rst*	*T* ft^1	*Max* ft^1	*T* ext^1	*T* rst^1	*T* ft^2	*Max* ft^2	*T* ext^2	*T* rst^2	*T* ft^3	*Max* ft^3	*T* ext^3	*T* rst^3
1994	7.1	4.4	8.7	7.0	7.5	5.0	11.7	8.2	7.3	6.1	14.7	10.5	6.9	5.8	16.0	14.4
1995	8.5	3.9	11.6	10.7	8.4	4.8	14.0	10.6	6.9	6.0	14.3	12.1	6.5	5.6	21.1	19.4
1996	6.0	2.5	9.8	8.8	6.2	2.5	10.2	9.2	6.7	4.7	12.5	11.1	7.3	6.4	18.7	17.7
1997	8.2	5.0	12.1	10.5	8.0	5.3	12.9	11.4	6.8	6.2	18.6	16.0	6.6	5.2	17.3	15.7
1998	8.2	3.9	8.7	10.2	7.7	3.3	8.4	8.5	8.4	4.7	10.3	11.3	6.8	5.8	14.6	17.4
1999	7.7	4.5	9.0	11.2	7.7	4.7	10.4	12.6	7.6	7.3	12.3	14.8	6.6	5.5	14.5	19.8
2000	4.7	2.7	7.5	11.5	6.0	4.5	10.9	15.6	6.6	5.8	13.5	18.4	6.6	5.5	13.2	20.2
2001	6.4	1.9	6.9	10.7	4.4	1.8	6.5	11.3	7.0	5.1	11.4	15.9	7.1	5.8	14.7	19.6
2002	6.0	2.9	8.8	12.4	6.7	4.0	10.8	14.4	6.9	6.1	11.4	16.4	6.7	5.5	11.7	19.1
2003	8.0	5.0	8.9	15.1	9.3	4.8	9.5	14.5	7.6	5.7	10.0	14.2	6.6	5.7	13.8	21.4
2004	6.3	2.8	7.5	12.9	6.4	2.9	8.5	14.3	7.3	5.8	9.1	16.7	6.8	5.8	13.0	19.5
2005	6.1	3.0	7.5	12.9	6.4	3.4	9.4	14.7	7.1	4.7	11.3	15.1	6.7	5.8	14.4	22.0
2006	5.6	3.0	6.4	12.1	5.5	3.0	7.4	13.4	7.7	6.4	10.3	15.0	6.7	5.8	15.2	22.8
2007	7.7	4.9	8.3	15.4	7.5	5.4	9.7	15.9	6.5	6.3	13.1	20.3	6.6	5.6	12.6	18.7
2008	4.7	1.6	6.7	8.4	6.2	4.3	11.1	17.3	6.5	5.9	13.4	18.1	7.0	5.8	13.9	19.8
2009	6.4	3.9	8.4	10.1	7.8	5.2	9.5	15.0	6.5	5.8	12.4	17.7	6.7	5.6	13.4	19.9
2010	6.5	2.6	6.3	12.8	6.8	3.3	7.5	13.1	7.3	5.9	9.2	16.8	6.8	5.5	14.6	21.2
2011	8.7	6.1	9.8	11.5	8.4	6.5	10.3	16.8	6.8	5.9	10.5	17.0	6.8	5.6	12.6	13.9
2012	6.3	2.7	6.3	8.0	7.5	3.8	10.5	15.5	6.8	5.3	13.0	18.0	7.0	5.3	17.8	19.1
2013	3.2	2.0	5.8	7.5	4.7	3.0	8.6	11.8	6.8	5.5	13.4	17.7	7.0	5.8	17.3	24.7
2014	8.0	4.4	10.3	14.1	7.7	4.4	10.5	14.2	7.8	6.3	12.3	16.8	6.7	5.6	16.6	22.0
2015	6.4	2.6	9.3	15.0	6.7	4.4	10.6	15.0	6.5	5.8	14.7	19.3	7.0	5.8	15.3	20.3
2016	5.3	2.2	7.9	12.2	6.3	4.9	11.1	14.0	6.8	6.4	14.7	20.5	7.7	6.3	15.9	21.6
2017	6.1	3.8	8.3	13.2	7.2	4.9	10.2	15.5	6.8	5.6	14.4	19.4	6.5	5.0	15.8	20.6
2018	6.1	3.1	8.9	12.9	6.4	4.3	12.0	17.5	6.7	6.2	15.6	20.1	6.8	5.4	17.6	22.4

Explanations: (*Max ft*)–(*Max* ft^3) — Maximal foraging times of the population (h/night) in Types 1–3 activity; (*T ext*)–(*T* ext^3) — External temperature (°C) in Types 1–3 activity; (*T rst*)–(*T* rst^3) — Roost temperature (°C) in Types 1–3 activity; (*T f t*)–(*T f* t^3) — Total foraging time (h/night) in Types 1–3 activity; All temperatures at midnight. Types 1–3 — Periods of bat activity deduced from bat movement in and out of the roost

larger (Williams, 1961; Taylor, 1973; Avery, 1985; Rydell, 1989). Also, insect density affected birth dates since the date of parturition of *Epesticus nilssonii* was dependent on the mean temperature during early summer when the aerial insect density was 0.1 m^3 or higher and it was energetically profitable to forage. The link between the duration of the threshold temperature and insect density was found by Rydell (1989) who reported that insect density was determined by air temperature and reached a threshold at 6–10°C although insects can fly at lower temperatures. Also, the gestation length of *Pipistrellus*, therefore the birth date, was dependent on temperature and food supply in a captive colony (Racey, 1973). However, environmental factors and foraging times in the spring did not explain 100% of the variance in the birth date ($R^2 = 54.5\%$). Therefore, there are other factors associated with the external and roost temperatures in summer may be associated with birth timing such as the length of the gestation period, the age at which the females became pregnant and /or whether the females were born early or late.

The effect of rain on birth timing varies according to species and a previous study at Stackpole showed that the mean birth date of *R. ferrumequinum* was not dependent on rain (McOwat and Andrews, 1995). Also, this study showed that *R. ferrumequinum* at Stackpole continued to forage during light rain since direct access from the roost to broadleaf woods provided cover and insect prey. The effect of light rain was incorporated in the maximal foraging time and the number of nights when *R. ferrumequinum* did not forage at all during heavy rain in April was less than 1.0% of the total in April and those nights were also colder than average. The effect of rain on foraging appears to be species specific since reproductive timing of *Myotis* species was selectively affected by a cool wet summer. *Myotis lucifugus* experienced delays whilst *M. keenii* was not affected, because this species was able to glean prey in cool wet conditions (Burles *et al.*, 2009) and Grindal *et al*. (1992) found similar results since high levels of precipitation delayed reproduction of not only *M. lucifugus* but also *Myotis yumanensis*.

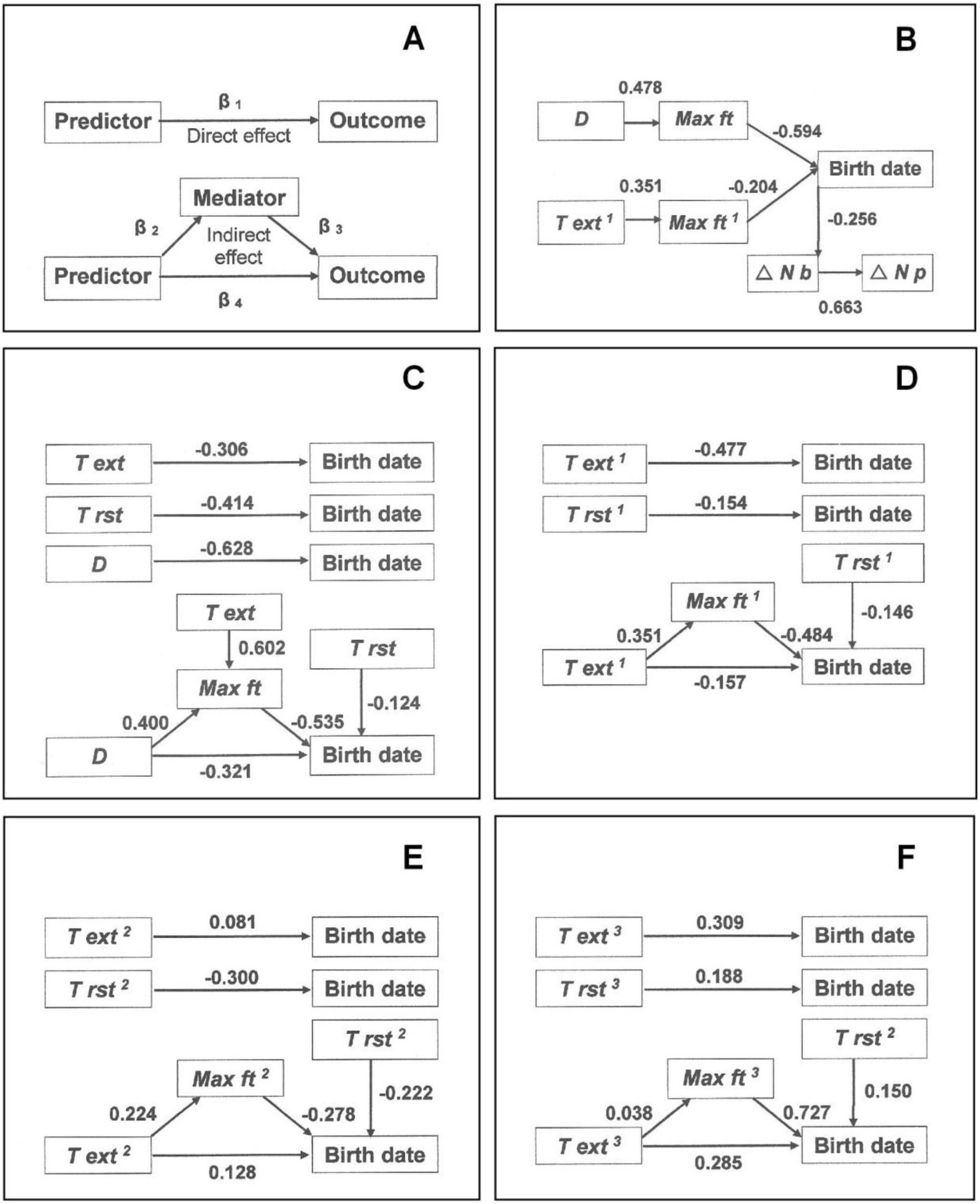

FIG. 3. Multivariate path analysis model results for direct and indirect relationships between variables in Types 1–3 of *R. ferrumequinum* activity at Stackpole nursery roost. A — Mediation model; B — Model pathway to show the effect of environmental factors on the year to year changes in the population; C–F — Path diagrams for bat activity; Types 1a, 1b, 2, and 3, respectively; β — Mean value of a path coefficient, *D* — Degree days, integrated air temperature in April, Environmental variables during bat activity, Types 1–3; *T ext* to $T\ ext^3$ — External temperature at midnight (°C); *T rst* to $T\ rst^3$ — Roost temperature at midnight (°C); *Max ft* to Max ft^3 — Maximal foraging times of the population (h)

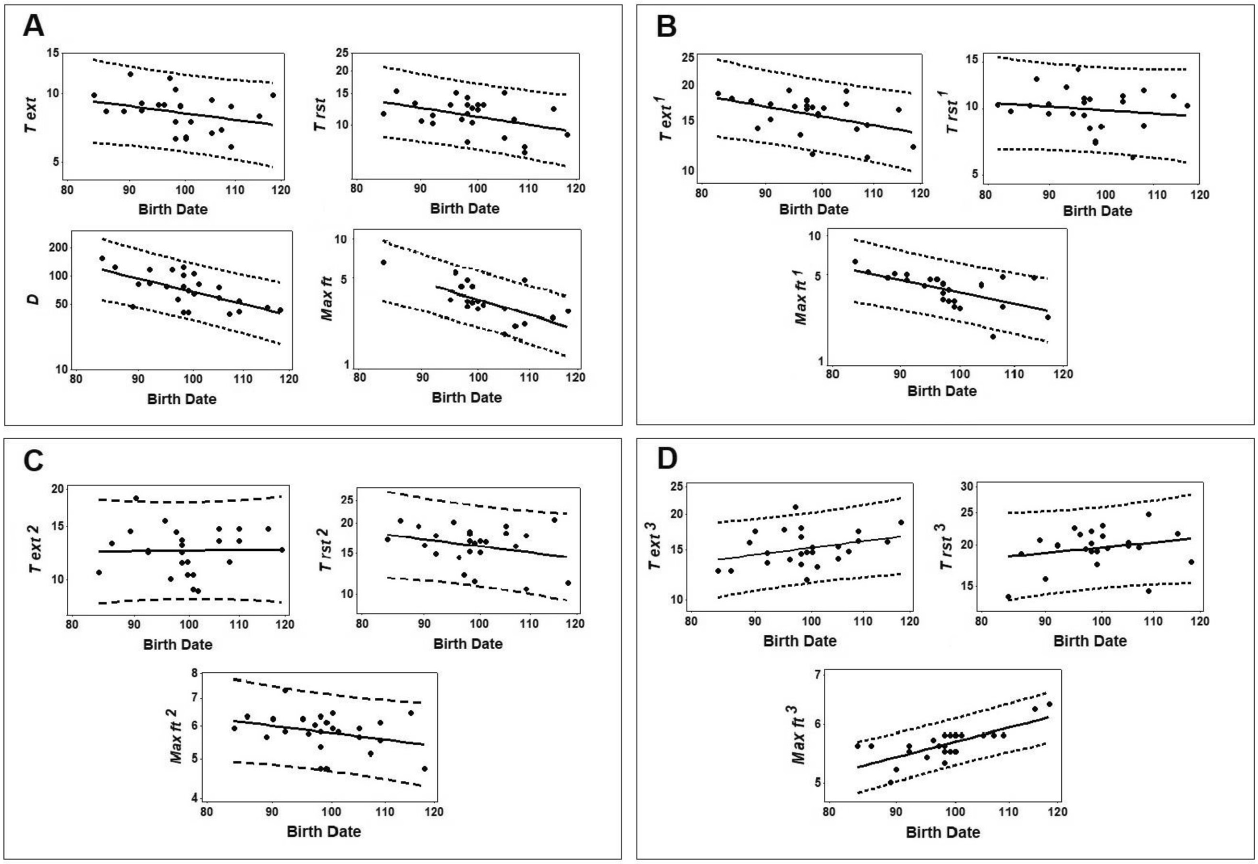

Fig. 4. Matrix plots based on data collected during *R. ferrumequinum* activity Types 1–3 at Stackpole, 1994–2018. A — April (Type 1a), B — April–May (Type 1b) , C — May–June (Type 2), D — June–July (Type 3). *T ext* to *T ext*^{3} — External temperature (°C), *T rst* to *T rst*^{3} — Roost temperature (°C), *Max ft* to *Max ft*^{3} (h) — Maximal foraging time, in Types 1–3. *D*, degree days, integrated air temperature in Type 1a. The 95% prediction intervals (—) around the fitted linear regression lines (—) predict that 95 out of a hundred new observations will fall within the upper and lower limits of the intervals. The matrix plot displays the direct effects of the log$_{10}$ transformed environmental factors associated with temperature (e.g., *T ext*, *T rst* and *D*) and the maximal population foraging time *Max ft* versus the birth dates of the pups (days after April 1). Scales on the *x*-axis are the log$_{10}$ number of days after April 1 in each year from 1994 to 2018 when half the number of the total of pups was born. A value of 2.0 on the *x*-axis corresponds 100 days after April 1. The scales on the *y*-axis are the log$_{10}$ transformations of the temperature-related environmental factors

Ransome (2008) proposed that abundance of prey in spring promoted rapid pregnancy of breeding females and Jones (1990) identified a *R. ferrumequinum* preference in the spring for male cockchafer prey, *Melolontha melolontha*, selected for prey size, optimal for foraging by echolocation. At Stackpole the main *R. ferrumequinum* prey species identified in spring from faecal droppings were crane flies, Tipulidae, and cockchafers, *Melolontha* (Ransome, 1997*a*) and both species have temperature dependent life cycles (Todd, 1996; Huiting *et al.*, 2006; Jourdan *et al.*, 2019). Adult *Melolontha* feed on tree leaves, mainly oak (Huiting *et al.*, 2006) and *R. ferrumequinum* forage in woodland in spring, which is warmer than pasture (Jones *et al.*, 1995; Ransome, 1997*b*). Aerial insects increase in abundance above the 10°C threshold level (Jones *et al.*, 1995) but in adverse weather conditions aerial prey were effectively selectively removed from the diet of female bats. At temperatures less than 12°C Lepidoptera and *Melolontha* were removed, followed by *Aphodius* then Tipulids and Trichopterans until at 5°C only Ichneumons were available. Consequently, pregnancies would be extended, birth dates would be later and milk supply to bats born before cool wet periods would be reduced (Ransome, 1997*a*).

According to the match-mismatch hypothesis proposed by Durant *et al.* (2007) the reproductive success of the predator, *R. ferrumequinum*, would be dependent on prey availability in April. Ransome (1995) observed that higher levels of key prey generated earlier births. A rise in *R. ferrumequinum* mortality following the lack of prey showed the significance of prey abundance on the population (Ransome and Priddis, 2005). Arlettaz *et al.* (2003) showed that

TABLE 3. Multivariate path model results. Direct and indirect effects of environmental factors in (A) Type 1a, (B) Type 1b, and (C) Type 2, and (D) Type 3 activity on birth dates, and (E) path model statistics to predict year to year changes in population

	Effect	Path			ß	SE	t = ß/SE	*P*	R^2 (%)
A	Direct	*T ext*	→	Birth date	-0.306	0.082	3.75	<0.001	
		T rst	→	Birth date	-0.414	0.076	5.43	<0.001	
		D	→	Birth date	-0.628	0.064	9.81	<0.001	
	Indirect	*T ext*	→	*Max ft*	0.602	0.063	9.55	<0.001	
		D	→	*Max ft*	0.400	0.098	4.08	<0.001	
		Max ft	→	Birth date	-0.535	0.098	5.45	<0.001	
		D	→	Birth date	-0.321	0.113	2.84	<0.001	
		T rst	→	Birth date	-0.124	0.095	1.30	0.189	
		Sobel's test: $Z = -3.27$, $P = 0.001$, R^2 (Birth date with mediation by *Max ft*) = 64.1%							
B	Direct	*T ext* ^{1}	→	Birth date	-0.447	0.081	5.55	<0.001	
		T rst ^{1}	→	Birth date	-0.154	0.069	2.23	0.026	
	Indirect	*T ext* ^{1}	→	*Max ft* ^{1}	0.351	0.088	3.99	<0.001	
		Max ft ^{1}	→	Birth date	-0.484	0.071	6.87	<0.001	
		T ext ^{1}	→	Birth date	0.157	0.075	2.09	0.002	
		T rst ^{1}	→	Birth date	-0.146	0.079	1.85	0.064	
		Sobel's test: $Z = -4.81$, $P < 0.001$, R^2 (Birth date with mediation by *Max ft* ^{1}) = 49.9%							
C	Direct	*T ext* ^{2}	→	Birth date	0.081	0.095	0.86	0.393	
		T rst ^{2}	→	Birth date	-0.300	0.143	2.10	0.035	
	Indirect	*T ext* ^{2}	→	*Max ft* ^{2}	0.224	0.089	2.52	0.012	
		Max ft ^{2}	→	Birth date	-0.278	0.112	2.48	0.013	
		T ext ^{2}	→	Birth date	0.128	0.103	1.25	0.213	
		T rst ^{2}	→	Birth date	-0.222	0.126	1.76	0.078	
		Sobel's test: $Z = -1.77$, $P = 0.077$, R^2 (Birth date with mediation by *Max ft* ^{2}) = 15.4%							
D	Direct	*T ext* ^{3}	→	Birth date	0.309	0.087	3.56	<0.001	
		T rst ^{3}	→	Birth date	0.188	0.105	1.78	0.075	
	Indirect	*T ext* ^{3}	→	*Max ft* ^{3}	0.038	0.061	0.62	0.535	
		Max ft ^{3}	→	Birth date	0.727	0.048	15.25	<0.001	
		T ext ^{3}	→	Birth date	0.285	0.057	5.03	<0.001	
		T rst ^{3}	→	Birth date	0.150	0.076	1.97	0.049	
		Sobel's test: $Z = 0.13$, $P = 0.893$, R^2 (Birth date with mediation by *Max ft* ^{3}) = 67.1%							
E	Direct	*D*	→	*Max ft*	0.478	0.082	5.85	<0.001	22.8
		T ext	→	*Max ft* ^{1}	0.698	0.057	12.14	<0.001	12.3
		Max ft	→	Birth date	-0.594	0.085	6.99	<0.001	35.3
		Max ft ^{1}	→	Birth date	-0.204	0.096	2.12	0.034	4.2
		Birth date	→	$\Delta N b$	-0.256	0.088	2.89	0.004	6.6
		$\Delta N b$	→	$\Delta N p$	0.663	0.060	11.10	0.001	44.0

Explanaions: *T ext*–*T ext* ^{3} — External temperature, *T rst*–*T rst* ^{3} — Roost temperature, *Max ft*–*Max ft 3* – Maximal population foraging time (Types 1–3 of activity), *D* — Degree days, $\Delta N b$ — Change in the number of births, $\Delta N p$ — Change in the number of adult females, ß — ß weights, standardized partial regression coefficients (strengths of the linear relationship between two variables), SE — Standard error, t = ß / SE – t (two-tailed *t* test), *P* — Probability value, R^2 — Coefficient of determination, closeness of data fitted to the regression line

cockchafer prey food availability influenced the timing of parturition of *Myotis blythii*, which was delayed on average 10 days later in years without cockchafers. A nursery roost population of *P. pygmaeus* was also dependent on prey availability in May–June because emergence of *Chironomus* spp. prey was temperature dependent (Andrews *et al.*, 2016). Ransome (1998) also attributed the birth date to variation in gestational length affected by insect supplies. *Rhinolophus ferrumequinum* born late had shorter forearm lengths (P. T. Andrews, T. P. McOwat, M. M. Andrews, P. Culyer, R. J. Haycock, A. N. Haycock, D. J. Harries, and N. P. Andrews, unpublished data) and adult wing size is dependent on pup forearm growth (Ransome, 1998), which had a large influence on whether the population grew or declined.

Riparian vegetation, woodland and distance from roosts play a key role in foraging habitat selection around colonies of *R. ferrumequinum* but also *M. emarginatus* (Dietz *et al.*, 2013; Fonderflick *et al.*, 2015). In this study maximal foraging times had a major influence on the birth dates and hence pups' chances of survival for the following year, and ultimately whether the population grew or declined. Also, in this study the average maximal foraging time in April (3.4 ± 1.2 h) would be sufficient for flight within 3–5 km from the nursery roost, i.e., within the foraging distance identified of non-lactating *R. ferrumequinum* (Stebbings, 1982; Jones *et al*. 1995; Duvergé, 1997; Billington, 2000 and 2001). Broad-leaved woodlands within 4 km of transitional roosts were also used by *R. ferrumequinum* in spring (Flanders and Jones, 2009). Short foraging periods of *M. lucifugus* were associated with cool nights and low prey density (Anthony *et al.*,1981). Foraging habitats such as broadleaf woods and grassland within the core sustenance zones with dense connected networks of green linear features hedgerows and tree lines favour *R. ferrumequinum* populations (Duvergé and Jones, 1994; Duvergé and Jones, 2003; Jones and Duvergé, 2003; Russo *et al.*, 2010; Dietz *et al*., 2013). These habitats are positively related to colony size, so it is imperative that cattle-grazed permanent pastures are preserved and that hedgerows are untrimmed for 3–10 years (Froidevaux *et al.*, 2017). Since hedgerows that were untrimmed for three years and the amount of semi-natural grassland within 0.5 km of sampling sites positively influenced *R. ferrumequinum* foraging (Froidevaux *et al.*, 2019). Also, the probability of *R. ferrumequinum* presence was higher when the distance between hedgerows was below 38 m and decreased rapidly when it was larger than 50 m (Pinaud *et al.*, 2018). Even linear features such as highly managed hedgerows surrounding arable fields were important for functional connectivity (Finch *et al.*, 2020).

Conservation policy for *R. ferrumequinum* at Stackpole includes maintaining suitable habitat to support the population with broad-leaved woodland, tree lines and hedgerows connecting the roost to insect rich grassland and open water (Countryside Council for Wales, 2008). Preservation of nursery roosts require consideration of environmental stresses and habitat especially the effect of agricultural organic matter and ammonia in water bodies (Ransome, 1997*b*; Duvergé and Jones, 2003; Jones *et al.*, 2009). The Stackpole SAC does not include ley farms that cultivate grasses and legumes in short term rotation of 2–5 years to improve soil fertility. Beetle species have been found in leys but there was a negative relationship between *R. ferrumequinum* activity and *Aphodius* and *Onthophagus* abundance (Anderson *et al.*, 2020). However, that study may not have included late summer and when juvenile *R. ferrumequinum* forage and *Aphodius* is the preferred prey (Ransome, 1997*a*).

Since climate change is a major issue (Parmesan and Yohe, 2003) changes in *R. ferrumequinum* populations are important. The mean birth date of *R. ferrumequinum* at Stackpole has occurred earlier since 1982. McOwat and Andrews (1995) recorded a mean birth date of 105.3 ±7.5 days from 1982–1991, in this study from 1994–2006, it was 100.4 ± 7.3 days and from 2006–2018 it was 98.2 ± 8.9 days. The range of *R. ferrumequinum* mean birth dates has also extended since Ransome (1998) observed a range of birth dates from 30 June to 27 July between 1973 and 1998, but in this study the range was from 23 June to 27 July. Also, Barclay (2012) identified a large variation in the birth dates of *Eptesicus fuscus*, which ranged from 13 June to 4 August, and the median birth date varied from 20 June to 14 July. The implications for this species are likely increases in the *R. ferrumequinum* population and possibly an expanded distribution. This study has demonstrated the importance of foraging areas around *R. ferrumequinum* nursery roosts and that in April, with external temperature, maximal population foraging time has a major influence of the birth dates and ultimately whether the population grew or declined.

SUPPLEMENTARY INFORMATION

Contents: Supplementary Appendix. Sample Excel spreadsheet for calculation of *R. ferrumequinum* pup birth dates form their forearm length measurements in 1995. Supplementary Information is available exclusively on BioOne.

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