

# Journal of Animal Ecology

DR DANIELLE MARIE LINTON (Orcid ID : 0000-0002-7854-8063)

DR DAVID W MACDONALD (Orcid ID : 0000-0003-0607-9373)

Article type : Research Article

Editor : Albert Phillimore

Section Heading: Climate Ecology

**Spring weather conditions influence breeding phenology and reproductive success in sympatric bat populations**

Danielle M. Linton<sup>a\*</sup> and David W. Macdonald<sup>a</sup>

<sup>a</sup> University of Oxford, Department of Zoology, Wildlife Conservation Research Unit (WildCRU), The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, OX13 5QL, UK

\*Corresponding author: danielleminton@gmail.com

## ABSTRACT

1. Climate is known to influence breeding phenology and reproductive success in temperate zone bats, but long-term population level studies and interspecific comparisons are rare.
2. Investigating the extent to which intrinsic (i.e. age), and extrinsic (i.e. spring weather conditions), factors influence such key demographic parameters as the proportion of females becoming

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2656.12832

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pregnant, or completing lactation, each breeding season, is vital to understanding of bat population ecology and life-history traits.

3. Using data from twelve breeding seasons (2006 - 2017), encompassing the reproductive histories of 623 *Myotis daubentonii* and 436 *M. nattereri* adult females, we compare rates of recruitment to the breeding population, and show that these species differ in their relative sensitivity to environmental conditions and climatic variation, affecting annual reproductive success at the population level.
4. We demonstrate that i) Spring weather conditions influence breeding phenology, with warm, dry and calm conditions leading to earlier parturition dates and advanced juvenile development, whilst cold, wet and windy weather delays birth timing and juvenile growth, ii) Reproductive rates in first-year females are influenced by spring weather conditions in that breeding season and in the preceding breeding season when each cohort was born. Pregnancy and lactation rates were both higher when favourable spring foraging conditions were more prevalent, iii) Reproductive success increases with age in both species, but at different rates, iv) Reproductive rates were consistently higher, and showed less inter-annual variation, in second-year and older *M. daubentonii* (mean 91.55%  $\pm$  0.05 SD) than *M. nattereri* (mean 72.74%  $\pm$  0.15 SD), v) Estimates of reproductive success at the population level were highly correlated with the size of the juvenile cohort recorded each breeding season.
5. Improving understanding of the influence of environmental conditions, especially extreme climatic fluctuations, and the identification of critical periods (i.e. spring for reproductive female bats in temperate zones), which have disproportionate and lasting impacts on breeding phenology and reproductive success at a population level, is critical for improving predictions of the likely impact of climate change on bat populations.

**Key-words** Age, Chiroptera, Climate, Individual-based models, Lactation, Life-history traits, Mammal, Pregnancy.

## INTRODUCTION

Climate is an important factor in the regulation of animal populations, and a key driver in phenology, the timing of biological events (Stenseth *et al.* 2002, Parmesan 2007). In seasonal environments the timing of events such as hibernation and breeding can be critical for survival and reproductive success (Sheriff, Buck & Barnes 2015). Few studies have examined the effects of climate-induced shifts in breeding phenology on population demographics or vital rates (Charmantier *et al.* 2008, Miller-Rushing, Høye, Inouye & Post 2010). Such information is crucial for predicting the impacts of climate change on the stability and conservation status of wild populations (Adams 2010, Sherwin, Montgomery & Lundy 2012).

Periods of climatic sensitivity have been identified, and rates of phenological change quantified, in many taxa across multiple trophic levels, however long-term datasets for mammal populations remain rare, and no suitable monitoring scheme data are currently available for bats (Boutin & Lane 2014, Thackeray *et al.* 2016). Our study demonstrates, for the first time in vespertilionid bats (the largest family in the order Chiroptera), that spring weather conditions, including extreme climatic fluctuations, do influence breeding phenology and reproductive success at the population level.

Over 20% of all mammal species are bats, and bats provide important ecosystem services around the world, including pollination, seed dispersal, and biological pest control (Altringham 2011). Despite their small size (wingspan less than 300 mm in our study species) bats can have exceptional longevity (e.g. over 30 years for some *Myotis* spp.) (Austad 2010), but population recoveries from unfavourable perturbations are known to be limited by low productivity (Ward, Ransome, Jones & Rossiter 2014). Female bats in the genus *Myotis* typically produce a single juvenile per breeding

season, with twins being exceptional (Altringham 2003). In temperate zones most bat species are monoestrous but the annual reproductive cycle is interrupted by hibernation (Altringham 2011). Mating occurs before and during winter (Rivers, Butlin & Altringham 2005, Encarnação 2012, Angell, Butlin & Altringham 2013) and females store sperm in the uterus and oviduct until ovulation in spring (Neuweiler 2000).

Spring weather conditions affect the duration of gestation and timing of parturition in temperate zone bats (Racey & Swift 1981, Ransome & McOwat 1994). Foraging efficiency is reduced by low temperatures, precipitation, and strong winds (Rydell 1989, Grindal, Collard, Brigham & Barclay 1992, Burles, Brigham, Ring & Reimchen 2009). These adverse conditions increase the thermoregulatory costs of foraging bouts, and decrease prey availability for insectivorous bats (Anthony, Stack & Kunz 1981, Racey & Swift 1981). Bats can conserve energy during unfavourable conditions by extended use of torpor (Willis, Brigham & Geiser 2006), but this also retards foetal development, prolonging gestation (Racey & Swift 1981, Ransome & McOwat 1994). During 'late' springs, with prolonged sub-optimal conditions, breeding females face a trade-off between the short-term benefits and longer-term negative consequences of employing torpor to delay parturition. During reproduction peak energy demand occurs during lactation and provision of maternal care to support postnatal growth of dependent juveniles. Breeding females employ torpor to delay peak energy demand until environmental conditions improve and prey availability increases as summer progresses (Arlettaz, Christe, Lugon, Perrin & Vogel 2001, Willis *et al.* 2006). However, delayed parturition can have subsequent 'knock-on' fitness and survival costs for both the mother and offspring (Ransome 1995), due to a reduction in the time available after weaning and pre-hibernation in which to accumulate sufficient fat reserves, during late summer and autumn, prior to the onset of winter (Thomas, Dorais & Bergeron 1990, Ransome & McOwat 1994). Juveniles born earlier in the preceding breeding season are more likely to return to their maternity colony and breed as first-year females (Frick, Reynolds & Kunz 2010). Earlier birth timing, given favourable

conditions, can also increase long-term survival rates and lifetime reproductive success (Ransome 1989, 1995).

Previous studies have demonstrated that parturition is often highly synchronised within maternity colonies of a single species, but that sympatric species can have differential responses to the same environmental conditions, probably due to inter-specific differences in dietary specialisation and prey availability (Arlettaz *et al.* 2001, Burles *et al.* 2009, Lučan, Weiser, & Hanák 2013). Our two study species, Daubenton's bat, *Myotis daubentonii* (Kuhl, 1817) and Natterer's bat, *M. nattereri* (Kuhl, 1817) are both widely distributed across the palearctic with significant range overlap (Dietz, Nill & von Helversen 2009) but niche partitioning with respect to habitat use and foraging strategies. *M. daubentonii* specialise in aerial hawking and trawling for insects over open water (Jones & Rayner 1988, Rydell Entwistle & Racey 1996). *M. nattereri* are adapted to hunting in cluttered environments, gleaning invertebrates from vegetation and cobwebs (Siemers & Schnitzler 2000).

Age is known to influence reproductive rates in temperate zone bats, with older experienced females being more successful than young inexperienced breeders (Lučan & Hanák 2011, Hood, Bloss & Kunz 2002), but empirical studies comparing age classes within the same population whilst simultaneously considering the influence of environmental conditions on reproductive rates are rare (Ransome 1995, Frick *et al.* 2010). Previous comparative studies of breeding success have been based on opportunistic captures, often with restricted sample sizes, of bats of unknown age (Burles *et al.* 2009, Adams 2010). To our knowledge, this is the first long-term study to be based on repeat sampling of known individuals, both within and across breeding seasons, incorporating data from a high proportion of two sympatric congeneric bat populations each breeding season, to produce robust comparative estimates of reproductive success per annum.

We predict that spring weather conditions (temperature, precipitation and wind) will influence breeding phenology and reproductive success within our study populations. Specifically, we examine whether:

- i) Spring weather conditions affect breeding phenology,
- ii) Pregnancy and lactation rates in first-year females are affected by spring weather conditions and differ between species. We expect favourable spring foraging conditions to increase the proportion of breeding attempts, and overall reproductive success, of first-year females,
- iii) Reproductive success increases with age in both species,
- iii) Spring weather conditions affect breeding phenology and reproductive success at the population level, but to a different extent per species. Cold, wet and windy spring weather is predicted to delay parturition and decrease breeding success, whilst warm, dry and calm spring conditions are predicted to advance parturition dates and increase breeding success.

## MATERIALS & METHODS

### Data Collection

Bats were found by day in roosts within Schwegler™ woodcrete boxes distributed across our study site, Wytham Woods (51°77'N, 1°33'W) as described by Perrins (1965) and August, Nunn, Fensome, Linton & Mathews (2014). Bats were extracted by hand and placed into cloth bags then examined and immediately returned to their roosts. Maternity colonies containing heavily pregnant females or non-volant juveniles were generally not handled to minimise disturbance. All ringing and handling was carried out under licence from the Statutory Nature Conservation Organisation (2017-29766-SCI-SCI and preceding project licences).

Our full dataset for ringed adult females comprises 12 years of data (2006 - 2017) detailing the reproductive histories of 623 *M. daubentonii* (individual bats were monitored for an average of  $2.93 \pm 2.52$  SD, range 1 - 11, breeding seasons per individual) and 436 *M. nattereri* (individuals were monitored for an average of  $3.50 \pm 2.71$  SD, range 1 - 11, breeding seasons per individual).

### *Biometric measurements*

Forearm length was measured to the nearest 0.1mm using dial calipers (n = 4925, 1 - 23 measurements per female). Weights were recorded to the nearest 0.1g using a spring balance (n = 4839, 1 - 24 measurements per female). Bats weighed from day roosts had not foraged for several hours, and most measurements were taken during the afternoon or evening (pre-emergence) to reduce weight variation attributable to food in the digestive tract.

### *Assessment of Age*

*M. daubentonii* and *M. nattereri* are born naked and blind, fur begins to develop at 3 - 5 days old, eyes open around 10 days old, up to two weeks old juveniles are typically wrapped within their mother's wing membrane within day roosts, often attached to the nipple. Forearm measurements from juveniles estimated to be 5 - 7 weeks of age (see Supplementary Fig S2) can be full grown (equal to adult measurements for that individual).

Juvenile bats were volant before handling and ringing was undertaken. Juveniles were identified by the presence of unfused metacarpal-phalangeal epiphyseal gaps (Hoying & Kunz 1998). Once finger joints were fully ossified, a suite of secondary characteristics was used, including fresh 'tacky' wing membranes, grey pelage and light weight (Adams 2010). We are confident these features are sufficiently diagnostic based on corresponding information being recorded almost exclusively from recaptured juveniles (of 435 ringed females identified as juveniles with fused epiphyses when recaptured; 97.93% (n = 426) were confirmed as juvenile based on ring history, only 2.07% (n = 9) were actually adults incorrectly identified as juvenile). Male bats were excluded from all analyses except forearm growth in juveniles (a measure of breeding phenology), and juvenile cohort size per breeding season.

Between 2006 to 2016, 233/510 female *M. daubentonii* and 214/318 female *M. nattereri* ringed as juveniles were recaptured as adults in subsequent breeding seasons. Only females ringed as

juveniles (age class = 0) then recaptured in the subsequent breeding season (age class = 1) when their pregnancy and/or lactation status could be assessed were included in our analyses of first-year females (models Ia and Ib).

Female bats of unknown age could often be identified as adult based on breeding status (i.e. parous nipple condition), or timing (if encountered before juveniles were volant) when first captured. When recaptured in subsequent breeding seasons a minimum age was calculated per bat of unknown age based on the number of years since being ringed, plus minimum age when ringed (confirmed adult at first capture = 1, uncertain whether adult or juvenile at first capture = 0).

To investigate the influence of age on reproductive success (model II) only bats of known age were included in age classes 1, 2 and 3 (first, second and third breeding seasons respectively since bats were juvenile). Data from all females of known and minimum age in their fourth breeding season or above were pooled to improve the representativeness of age class  $\geq 4$  through inclusion of more and possibly older bats. The upper limit of known age individuals in our dataset is 11 years, bats of unknown (minimum) age may actually be much older.

To include a higher proportion of the adult female breeding population when investigating inter-annual variation in reproductive success (model III) age classes 1 (known age, first breeding season as an adult) and  $\geq 2$  (bats of known and minimum age in their second breeding season or above) were used.

#### *Assessment of Reproductive Condition*

Each breeding season all adult females known to be alive were assigned a pregnancy status (pregnant, not pregnant, or unknown) and a lactation status (lactating, non-lactating, or unknown).

Pregnancy or non-pregnancy was determined by visual inspection of the abdomen (palpation was not usually necessary or more accurate), assessment of nipple condition (often diagnostic in primiparous females due to hormones inducing swelling during pregnancy), and bat weight early in



the season (pre-parturition). If bats were not examined until post-parturition a 'pregnant' status could be inferred if bats were found to be lactating or post-lactating. However, non-breeders and failed breeders lacking clear evidence of their breeding attempt that season were then recorded as 'unknown' pregnancy status. Few clear cases of non-breeding in older females (at least two years old) were recorded and for this reason we consider pregnancy rates from older females to be biased, underrepresenting non-breeders (see Supplementary Table S1). We therefore excluded pregnancy data for older females from our analyses. Pregnancy rates in first-year females are more reliable as nulliparous (not pregnant) and primiparous females (pregnant, even if their first breeding attempt subsequently failed) could be distinguished during the post-parturition period.

Lactation was identified based on enlarged mammary glands and hair loss around the nipples. Post-lactation was recorded when evidence of recent hair re-growth could be discerned. Bats lacking obviously swollen nipples, hair loss or recent re-growth around the nipple were classed as non-breeders, or failed breeders if previous captures had recorded evidence of pregnancy or lactation that season. Bats found to be post-lactating before juveniles could have been successfully weaned were also classified as failed breeders in that season. Distinguishing reliably between non-breeders and failed breeders was not always possible, depending on the timing and frequency of captures per individual per breeding season, so these categories were combined in our analyses. An 'unknown' status (excluded from our analyses) was recorded if bats were not encountered that breeding season but were subsequently found to be alive, or if the breeding status of an individual was ambiguous. By autumn non-breeders and failed breeders could not be reliably distinguished from successful breeders (some post-lactating females can appear to be nulliparous within a month of weaning their offspring). Lactation or recent post-lactation observed as juveniles were becoming volant and independent, were our indicators of apparently successful breeding attempts.

In our analyses lactation was treated as a binary response variable, with lactating = 1 corresponding to reproductive success, i.e. completion of lactation concurrent with weaning of offspring, and non-lactating = 0 encompassing non-breeders and failed breeders in that breeding season.

The proportion of adult females recorded as successful breeders was highly correlated with juvenile cohort size (no. bats ringed as known age = 0) each season (2010 - 2017), in both *M. daubentonii* (parameter estimate = 373.68, SE = 68.41,  $F_{1,6} = 29.84$ ,  $P = 0.002$ ,  $r^2 = 0.83$ ) and *M. nattereri* (parameter estimate = 149.81, SE = 20.35,  $F_{1,6} = 54.22$ ,  $P = <0.001$ ,  $r^2 = 0.90$ ).

### *Breeding Phenology*

Mean estimated parturition date, per species per breeding season, was used as a measure of breeding phenology. Parturition dates were estimated based on visual assessment of the age of non-volant juveniles observed within maternity colonies (see Supplementary Fig S1).

The first date per year when the forearm measurement of a juvenile was equal to the mean adult forearm size for that individual (based on comparison with subsequent repeat measurements), was recorded, per species, as an additional phenological indicator (see Supplementary Fig S2).

### *Meteorological data*

Hourly weather data were obtained from the Environmental Change Network (ECN) automated weather station at Wytham (data citation code: 'ECN:DL3/15'). The temporal availability of suitable foraging conditions (SFC) for bats was calculated by giving each hour of night a weighting of 1 if conditions were considered to be optimal (temperature greater than or equal to 10°C, rainfall less than 0.25 mm, maximum windspeed less than 4.0 ms<sup>-1</sup>), 0.5 if any criteria were sub-optimal (temperature between 7 - 10°C, rainfall between 0.25 - 0.75 mm, maximum windspeed between 4 - 5 ms<sup>-1</sup>) and 0 if any criteria were unsuitable (temperature less than 7°C, rainfall above 0.75mm,

maximum windspeed above 5 ms<sup>-1</sup>). Sunset and sunrise times were obtained from [www.SunriseSunset.com](http://www.SunriseSunset.com) for our study site. Hours following sunset and before sunrise were included or excluded as night length varied (see Supplementary Fig S3) and weighted as 0.5 if conditions were optimal, 0.25 if any criteria were sub-optimal, and 0 if any criteria were unsuitable. The criteria and thresholds selected were based on existing information relating bat activity levels to environmental conditions (Anthony *et al.* 1981, Ransome & McOwat 1994, Linton 2009).

Despite night length increasing from October to December the temporal availability of suitable foraging conditions for bats becomes less predictable, more variable, and decreases markedly, from over 6 hours per night to less than 2 hours per night on average, over the same period, remaining low (below 2 hours per night on average) through January to March. The temporal availability of suitable foraging conditions begins to increase again in April but is less predictable, more variable, and more restricted (below 3 hours per night on average) than throughout May to September (from 4 to over 8 hours per night on average) (see Fig 1 and Supplementary Fig S4). The cumulative total of night hours fulfilling the SFC criteria (based on weightings described above) during April each year (mean 73.65 ± 29.13 SD, during 1992 - 2017) was divided by the total duration of night in April (259 hours) to produce an April SFC Index (ASFC) per annum (mean 0.284 ± 0.11 SD, during 1992 - 2017). ASFC was selected as our measure of spring weather conditions each breeding season as April represents a critical time period when bats from our study populations emerge from hibernation and seek to gain condition whilst suitable foraging conditions may still be temporally restricted. See also Jan *et al.* (2017) regarding the temporal resolution of climatic variables, which identified April as a critical period influencing bat fecundity based on colony emergence counts. ASFC is largely determined by temperature, with rain and wind having comparatively little effect (see Supplementary Table S7). ASFC was a superior explanatory variable compared to mean April temperature (°C) in linear regression models with measures of breeding phenology as the response variable (see Supplementary Table S8).

## Data Analysis

### *Spring weather conditions and breeding phenology*

Linear regression was used per species to assess whether our two metrics of breeding phenology were associated with ASFC per breeding season.

### *Evidence of breeding in first-year females related to species and spring weather conditions*

Pregnancy (model Ia) and lactation (model Ib) in first-year females were treated as binary response variables (pregnant = 1, not pregnant = 0, and lactating = 1, non-lactating = 0, respectively) in separate logistic models (details of model selection are presented in Supplementary Tables S2 and S3), with species (SPP = *Myotis daubentonii* abbreviated to Md, and *M. nattereri* abbreviated to Mn) as a categorical explanatory variable, and spring weather conditions during their first breeding season as adults (ASFC), and for the year of their own birth (ASFC of the preceding breeding season = PSFC) as continuous explanatory variables. We also tested for interactions between SPP:ASFC and SPP:PSFC in case the effect of weather covariates differed between species. Calendar year as a factor (FYR) was included as a random intercept effect to ensure the correct level of replication was used in tests of year-level effects.

### *Reproductive success and age*

To investigate the influence of age on reproductive success (model II) we used generalized linear mixed models (GLMMs) with lactation as a binary response variable (lactating = 1, non-lactating = 0), species (SPP = Md and Mn) and four age classes (ACL = 1, 2, 3, and  $\geq 4$ ) as categorical explanatory variables, and ASFC and PSFC as continuous explanatory variables. We also tested for interactions between SPP:ACL, SPP:ASFC, SPP:PSFC, ACL:ASFC and ACL:PSFC in case the influence of age or weather covariates differed between species, or the effect of weather covariates differed with age (see Supplementary Table S4). Because this dataset contained repeat measures (each individual was

observed for between 1 - 11 breeding seasons across 2007 - 2017), individual (IND = ring number, a unique identifier per individual) was included as a random intercept effect, as was fYR, to ensure the correct level of replication.

#### *Inter-annual variation in reproductive success*

The influence of spring weather conditions (model III) was investigated using a subset of the data, from 2010 - 2017, to maximise sample size and therefore representativeness of the adult breeding population per season (see Supplementary Tables S5 and S6). Data from 2006 - 2009 were excluded from this analysis due to most adult females being of unknown age (minimum age 0 or 1, which were excluded from all analyses) during these seasons as the population was being ringed. Between 2006 - 2009 only 133/341 *M. daubentonii* and 222/401 *M. nattereri* breeding season records were from bats known to be in age classes 1 or  $\geq 2$ , compared to 1295/1490 *M. daubentonii* and 1082/1126 *M. nattereri* breeding season records from 2010 - 2017. For model III we used GLMMs with lactation as a binary response variable (lactating = 1, non-lactating = 0), species (SPP = Md and Mn) and two age classes (ACL = 1 and  $\geq 2$ ) as categorical explanatory variables, and ASFC and PSFC as continuous explanatory variables. We again tested for interactions between SPP:ACL, SPP:ASFC, SPP:PSFC, ACL:ASFC and ACL:PSFC (see Supplementary Table S6). Because this dataset contained repeat measures (range 1 - 8 breeding seasons per individual, across 2010 - 2017), IND was included as a random intercept effect, as was fYR, to ensure the correct level of replication.

#### *Model selection*

Statistical analyses were performed in R (R Core Team 2017), using the base 'lm' function, and the 'glmer' function in package lme4 (Bates, Maechler, Bolker & Walker 2015) for GLMMs. Model selection was based on Akaike Information Criterion corrected for small sample size (AICc) and model weights using package AICcmodavg (Mazerolle 2016) in accordance with an Information-Theoretic approach (Burnham & Anderson 2002).

## RESULTS

### *Spring weather conditions and breeding phenology*

Mean estimated parturition dates were negatively correlated (advanced) with ASFC in both *M. daubentonii* (parameter estimate = -59.50, SE = 6.08,  $F_{1,6} = 95.88$ ,  $P = <0.001$ ,  $r^2 = 0.94$ ) and *M. nattereri* (parameter estimate = -70.73, SE = 10.77,  $F_{1,6} = 43.16$ ,  $P = <0.001$ ,  $r^2 = 0.88$ ). The date when the first full grown juvenile was recorded each breeding season was also negatively correlated with ASFC in both *M. daubentonii* (parameter estimate = -57.98, SE = 16.68,  $F_{1,6} = 12.08$ ,  $P = 0.013$ ,  $r^2 = 0.69$ ) and *M. nattereri* (parameter estimate = -61.29, SE = 19.64,  $F_{1,6} = 9.74$ ,  $P = 0.021$ ,  $r^2 = 0.62$ ) (see Fig 2).

Mean estimated parturition dates within our dataset (2010 - 2017) varied by 30 days in *M. daubentonii* (earliest: 24/05/2011, and latest: 23/06/2012) and 38 days in *M. nattereri* (earliest: 02/06/11, and latest: 10/07/2012) (see Supplementary Fig S2). Mean estimated parturition dates were on average 9.75 ( $\pm 3.62$  SD) days earlier per breeding season in *M. daubentonii* compared to *M. nattereri*. The first confirmed full-grown juveniles of both species were typically recorded six weeks after mean estimated parturition dates per breeding season (see Figs 2 and S2).

### *Evidence of breeding in first-year females related to species and spring weather conditions*

Pregnancy rates in first-year females (model 1a) were significantly higher in *M. daubentonii* than *M. nattereri* (see Table 1). The probability of pregnancy in both species was positively associated with PSFC (see Figure 3a). The effect of ASFC differed between species (see Table 1), with a strong positive association in *M. nattereri*, but no effect in *M. daubentonii* (see Figure 3b).

Reproductive success in first-year females (model 1b) was also significantly higher in *M. daubentonii* compared to *M. nattereri* (see Table 1). The effect of PSFC differed between species, with a positive

association in *M. nattereri*, but no effect in *M. daubentonii*. There was a strong positive association between lactation rates and ASFC (see Figure 3c).

Pregnancy and lactation rates in first-year *M. nattereri* were both positively associated with both PSFC and ASFC. In contrast, pregnancy rates in first-year *M. daubentonii* were positively associated with PSFC but not ASFC, whereas lactation rates were positively associated with ASFC but not PSFC.

#### *Reproductive success and age*

Reproductive success increased with age (see model II in Table 1). Lactation rates were consistently higher in *M. daubentonii* relative to *M. nattereri* of equivalent age class (see Figure 4 and Supplementary Table S1). Lactation rates were positively associated with ASFC, but an influence of PSFC, or any interaction terms, was not well supported by model selection (see Supplementary Table S4).

#### *Inter-annual variation in reproductive success*

During 2010 to 2017, mean reproductive success in first-year *M. daubentonii* was 0.28 (0 - 0.86 minimum to maximum range), compared to 0.92 (0.81 - 0.97) for older *M. daubentonii*. Mean reproductive success in first-year *M. nattereri* was 0.12 (0 - 0.38), compared to 0.73 (0.51 - 0.93) for older *M. nattereri* (see Figure 5 and Supplementary Table S5).

Reproductive success varied between species, and age class, and there was strong evidence of a positive association with ASFC (see model III in Table 1, and Figure 3d), but an influence of PSFC, or any interaction terms, was not well supported by model selection (see Supplementary Table S6).

## DISCUSSION

Favourable spring weather conditions (warm, dry and calm nights providing suitable foraging conditions for bats) were associated with earlier parturition dates and increased reproductive

success in both study species. Pregnancy rates in first-year females increased when spring weather conditions were favourable in the preceding breeding season, when each cohort was born, and lactation rates increased with favourable spring weather conditions during their first breeding season as adults. Reproductive success increased with age in both species, but reproductive success per age class was consistently higher in *M. daubentonii* than in *M. nattereri*.

Despite similar rates of phenological change observed in response to fluctuating environmental conditions, with an advance in parturition dates of  $5.45 (\pm 0.80 \text{ SE})$  days per  $^{\circ}\text{C}$  in *M. daubentonii*, and  $6.56 (\pm 1.13 \text{ SE})$  days per  $^{\circ}\text{C}$  in *M. nattereri*, reproductive success at the population level per breeding season was higher and less variable in *M. daubentonii* than in *M. nattereri*. This finding has wider relevance to research attempting to quantify phenological change and predict impacts on wild populations (Miller-Rushing *et al.* 2010, Thackeray *et al.* 2016) by illustrating that equivalent shifts in the relative timing of biological events can have different impacts on key demographic rates and life-history traits, even in closely related species within the same community.

#### *Reproductive rates of first-year females in relation to species and spring weather conditions*

Some juveniles may not reach sexual maturity during their first autumn (Entwistle, Racey & Speakman 1998), especially in *M. nattereri* which are usually born one to two weeks later than *M. daubentonii* in our study populations and therefore have less time to fully develop pre-hibernation. Higher proportions of immature first-year *M. nattereri* than *M. daubentonii* within our study populations may partially explain the lower pregnancy rates we observe in *M. nattereri*. However, spring weather conditions (ASFC) were positively associated with the proportion of pregnant first-year *M. nattereri* per breeding season which suggests that rates of ovulation and gestation in sexually mature first-year *M. nattereri* are influenced by environmental conditions early in the breeding season, i.e. the ability to forage successfully (due to favourable weather and adequate prey availability) and gain condition upon emergence from hibernation. In contrast there was no detectable effect of ASFC on pregnancy rates in *M. daubentonii*, but spring weather conditions in the



preceding season (PSFC) were positively associated with pregnancy rates in both species. Earlier parturition dates increase the probability of juvenile females attempting to reproduce in the subsequent breeding season (Frick *et al.* 2010). Lactation rates in first-year females were positively associated with ASFC in both species.

#### *Reproductive success in relation to species, age, and spring weather conditions*

In both species, reproductive success was particularly low in first-year females (see Figs 4 and 5). Young females may be less efficient foragers (Hood *et al.* 2002), and therefore unable to maintain condition and sustain the high energetic demands of lactation and provision of maternal care to dependent offspring during the postnatal growth period. In addition to some being immature, or in poor condition, inexperienced mothers may provide poor maternal care and become failed breeders for behavioural reasons. For example, first-year females can be less synchronised during gestation than older females. First-year females are often the most advanced (obviously pregnant) bats early in breeding seasons with poor spring weather conditions. Conversely, first-year females also produce the last, often undersized, juveniles born within our study populations (DML unpublished data). We hypothesise that such asynchronies in reproductive timing result from failure to employ torpor to delay gestation in the former individuals, and late ovulation or retarded foetal development, due either to poor maternal condition or failure to maintain homeothermy to the same extent as experienced breeders, in the latter individuals. In both scenarios, juvenile survival is low; mothers are re-encountered as failed breeders, whilst their offspring are not re-encountered or are found dead or abandoned (DML personal observations).

Reproductive success increased with age in both species, although this increase was more gradual in *M. nattereri* (up to 4 years of age) than *M. daubentonii* (high from 2 years onwards). Adult female *M. daubentonii* are smaller (mean forearm 37.6 mm  $\pm$  1.15 SD) but heavier (mean weight 9.3 g  $\pm$  0.84 SD) on average than *M. nattereri* (mean forearm 39.1 mm  $\pm$  1.14 SD, mean weight 8.1 g  $\pm$  0.69 SD) (DML unpublished data). Although body size indicators and mass may be poor predictors of energy

reserves and fat stores (Green 2001), higher proportions of *M. nattereri* appear to experience poor body condition to the extent that breeding attempts fail. Underweight females suffering from hair loss (balding stress) whilst lactating (or post-lactating if failed breeders) have been encountered more frequently in *M. nattereri* than *M. daubentonii* (DML personal observations).

By influencing breeding phenology, specifically the timing of parturition, spring weather conditions can have a disproportionate and lasting effect on breeding success in temperate zone bats (Ransome 1989, Ransome & McOwat 1994, Frick *et al.* 2010), but species differ in their relative sensitivity to climatic variation, possibly mediated by niche partitioning and differences in foraging strategy (Arlettaz *et al.* 2001, Burles *et al.* 2009). The comparative difference in breeding phenology we observe, with parturition typically occurring one to two weeks earlier in *M. daubentonii* than *M. nattereri* within our study populations, is probably related to the extent to which spring weather conditions influence prey availability. Aquatic insects, an important component of *M. daubentonii* diet, may be less affected by air temperatures than terrestrial invertebrates (Syme, Fenton & Zigouris 2001). The effects of climate and phenological variation on prey abundance within our study system remain unknown.

More female *M. nattereri* than *M. daubentonii* have been encountered during April and May within our study system ( $n = 613$  females in 60 roosts, and  $n = 212$  females in 25 roosts, respectively), so differences in the timing of emergence from hibernation are unlikely to explain the differences in breeding phenology we observe. Roost micro-climate, and the size of maternity clusters, can both influence the energetic costs of maintaining heterothermy during gestation, lactation, and postnatal growth in juveniles (Syme *et al.* 2001, Willis & Brigham 2007, Pretzlaff, Kerth & Dausmann 2010). Day roost group sizes recorded within our study system are similar between species (mean group size  $11.15 \pm 8.12$  SD, range 1 - 42 bats,  $n = 637$  roosts in *M. nattereri*, and mean group size  $9.66 \pm 7.08$  SD, range 1 - 45 bats,  $n = 722$  roosts in *M. daubentonii*). However, differences in box occupancy rates, compared to use of alternative roosts (e.g. in trees and buildings) where group sizes are

unknown, make it unfeasible to assess the importance of roost ecology to the differences in breeding phenology that we observe using available data.

Determining the extent to which key demographic parameters, such as reproductive success, are influenced by environmental conditions and climatic variation is crucial for predicting the consequences of climate change on long-term population dynamics and stability. April 2011 was the warmest since records began in 1659, according to the Hadley Centre Central England Temperature dataset (Parker, Legg & Folland 1992). April 2012 was the wettest ever recorded at the Oxford Radcliffe Meteorological Station (based on data from 1767 - 2015) with 143 mm of rainfall recorded in Oxford (White 2016) and 141.6 mm at Wytham (approximately 5km west). These extreme climatic fluctuations contributed to the largest inter-annual variation in reproductive success of older females (age class  $\geq 2$ ) observed in our dataset, with a 16.05% reduction in *M. daubentonii* (from 97.30% down to 81.25%), and a 42.50% reduction (from 93.10% to 50.60%) in *M. nattereri*.

Inter-annual variation in reproductive success of first-year females is complicated by a 'lag-effect'; with spring weather conditions in the preceding breeding season (PSFC), influencing pregnancy rates in both species and lactation rates in *M. nattereri*. Breeding success was higher for first-year *M. daubentonii* in 2016 than in 2013 (despite similar ASFC in those years) because the cohort born in 2015 had earlier parturition dates, and consequently more time to mature and gain body condition prior to hibernation, than the cohort born in 2012. Similarly, more first-year *M. nattereri* reproduced in 2015 than in 2014 (despite 2014 having a higher ASFC than 2015) precisely because the cohort born in 2014 had earlier parturition dates than the cohort born in 2013.

Weaning of juveniles occurs shortly after the onset of volancy (Hamilton & Barclay 1998). Our measure of reproductive success (lactation or recent post-lactation as juveniles are becoming independent) certainly represents substantial maternal investment and reproductive effort by apparently successful breeders. Our estimates of reproductive success each breeding season (2010 - 2017), appear to be representative of our study populations, being highly correlated with juvenile

cohort sizes recorded per annum. Previous studies have failed to detect any such correspondence (Burles *et al.* 2009, Frick *et al.* 2010), or between breeding phenology, which was influenced by April temperatures, and reproductive success (Lučan *et al.* 2013).

Previous studies reporting reproductive rates in vespertilionid bats have pooled data from all reproductive categories (pregnancy, lactation and post-lactation), collected across the breeding season (Grindal *et al.* 1992, Burles *et al.* 2009, Adams 2010, Frick *et al.* 2010) or based on cross-sectional sampling at large maternity colonies (Lučan *et al.* 2013, Zeale *et al.* 2014). Our longitudinal data (repeat sampling of some individuals across a breeding season) indicate that previous estimates of reproductive rates in bats may therefore be biased, overestimating breeding success, as some failed breeders will not have been identified and accounted for as such. Few previous studies have included an unknown reproductive category or acknowledged that it is not always possible to make a reliable assessment (Adams 2010, Chauvenet, Hutson, Smith & Aegerter 2014, Zeale *et al.* 2014). Sampling bats of unknown age may also skew estimates, e.g. if young females are over-represented, or if nulliparous females are excluded (see Lučan *et al.* 2013).

Our study demonstrates, for the first time in vespertilionid bats (the largest family in the order Chiroptera), that spring weather conditions affect breeding phenology, recruitment rates, and reproductive success at the population level. Inter-annual variation in breeding success was more pronounced in *M. nattereri* than *M. daubentonii*, which may have long-term implications for population stability and community composition within our study system, and demonstrates that even congeneric species at the same trophic level can have markedly different responses to the same environmental conditions. Improving understanding of the impact of climatic variation, especially extreme fluctuations, and the identification of critical periods (e.g. spring for reproductive female bats in temperate zones) which have disproportionate and lasting impacts on population dynamics and life-history traits, is crucial for improving predictions of the likely impact of climate change on the stability and conservation of wild populations (Adams 2010, Sherwin *et al.* 2012).

### **Author's contributions**

DML conceived the project aims and objectives; DML and DWM agreed the methodology; DML collected and analysed the data, and wrote the manuscript. DWM contributed critically to drafts and gave final approval for publication.

### **Acknowledgements**

The authors would like to thank all volunteers and students who assisted with data collection. Dr Fiona Mathews (Chair of The Mammal Society) for enabling DML to act as an accredited agent on Natural England Project Licence 2017-29766-SCI-SCI and preceding licences. Nigel Fisher, Conservator of Wytham Woods, and his staff for their help and support. The Edward Grey Institute (EGI) researchers and field assistants for their collaboration and access to field equipment. Dr Paul Johnson (WildCRU) for modelling advice. We also thank Dr Marco Rughetti and other reviewers for their comments which helped improve this manuscript. This work was generously supported by a grant to DWM from S. Durie, with additional support from the Peoples' Trust for Endangered Species (PTES).

### **Data Accessibility**

- Data summary: uploaded as online supporting information (Tables S1 and S5)
- Model selection: uploaded as online supporting information (Tables S2, S3, S4, and S6)
- Data files and R script available from the Dryad Digital Repository:  
<https://doi.org/10.5061/dryad.h7m5f83>

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**Table 1.** Summary of top-ranked Generalized Linear Mixed Models (GLMMs) based on model selection (see Supplementary Tables S2, S3, S4 and S6). Model Ia = Pregnancy and Ib = Lactation in first-year females. Model II = Reproductive Success and Age, and Model III = Inter-annual variation in Reproductive Success.

**Figure 1.** Index of Suitable Foraging Conditions (SFC) per month (based on CEH Wytham automated meteorological station data from 2006 - 2016). Mean hours per night fulfilling SFC criteria (with  $\pm 1$  SD error bars) (white bars), and mean night length (grey bars).

**Figure 2.** Mean estimated parturition dates (open symbols), and date when the first full grown juvenile was recorded (filled symbols) per breeding season in *M. daubentonii* (circles) and *M. nattereri* (triangles) plotted against the proportion of total night hours with suitable foraging conditions in April (ASFC).

**Figure 3.** The effect of suitable foraging conditions on reproductive rates: a) PSFC and pregnancy of first-year females, b) ASFC and pregnancy of first-year females, c) ASFC and lactation in first-year females, and d) ASFC and lactation in second-year and older females.

**Figure 4.** Proportion of female *M. daubentonii* (circles) and *M. nattereri* (triangles) recorded as pregnant (P) or lactating (L) across different age classes (1 = first-year, 2 = second year, 3 = third year,  $\geq 4$  = fourth year or above).

**Figure 5.** Proportion of *M. daubentonii* (circles) and *M. nattereri* (triangles) lactating each breeding season per age class: first-year females (open symbols with no line because each cohort comprises unique individuals), and second-year and above (filled symbols connected by dashed lines). The proportion of total night hours with suitable foraging conditions in April (ASFC) is represented by a dashed line and  $\propto$  symbol.

**Table 1**

	<b>Model Ia</b>	<b>Model Ib</b>	<b>Model II</b>	<b>Model III</b>
Response variable:	Preg	Lact	Lact	Lact
Explanatory variable (SE):				
(Intercept)	-0.11 (0.86)	-3.44 (0.74)***	-2.69 (0.28)***	-0.85 (0.21)***
SPP(Mn)	-3.19 (0.89)***	-3.14 (0.93)***	-1.59 (0.19)***	-1.63 (0.18)***
ACL(2)			3.05 (0.26)***	
ACL(3)			3.57 (0.29)***	
ACL(≥4)			4.31 (0.24)***	
ACL(≥2)				2.76 (0.15)***
ASFC	1.66 (2.18)	7.85 (1.40)***	5.60 (0.65)***	6.00 (0.62)***
SPP(Mn):ASFC	6.98 (2.84)*			
PSFC	4.03 (1.41)**	0.56 (1.45)		
SPP(Mn):PSFC		5.20 (2.52)*		
No. Observations	231	318	1490	1642
No. Years (fYR)	11	11	11	8
Variance fYR (Intercept)	0.01	0.00	0.00	0.00
No. Individuals (IND)			606	656
Variance IND (Intercept)			0.84	0.76

\* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$

Figure 1

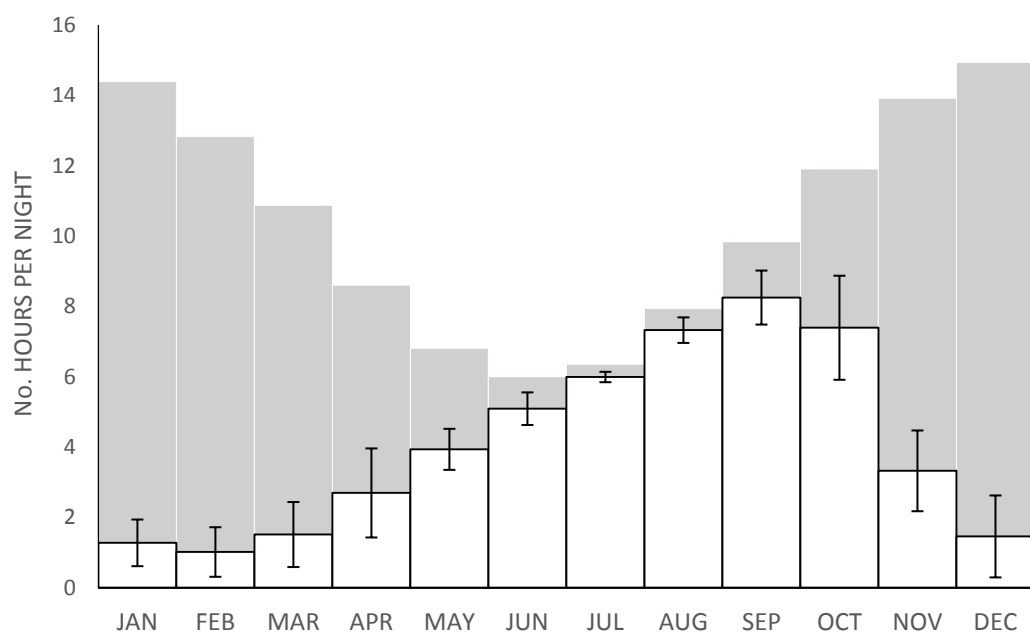
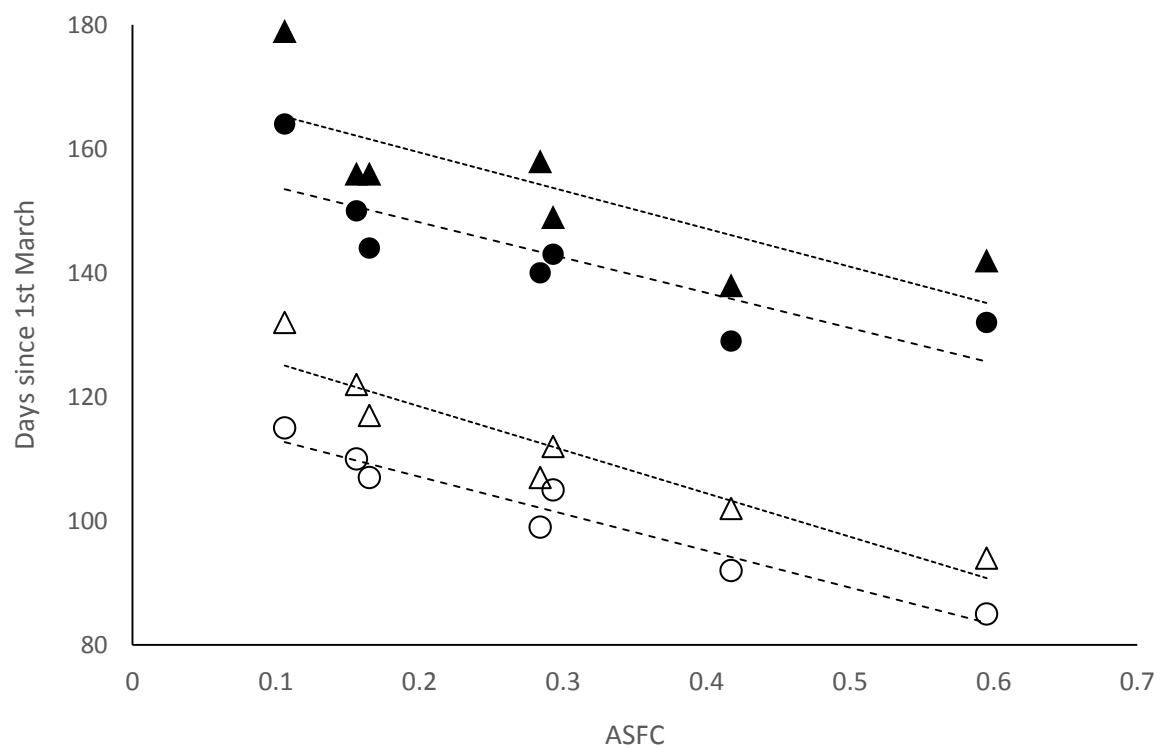


Figure 2



**Figure 3**

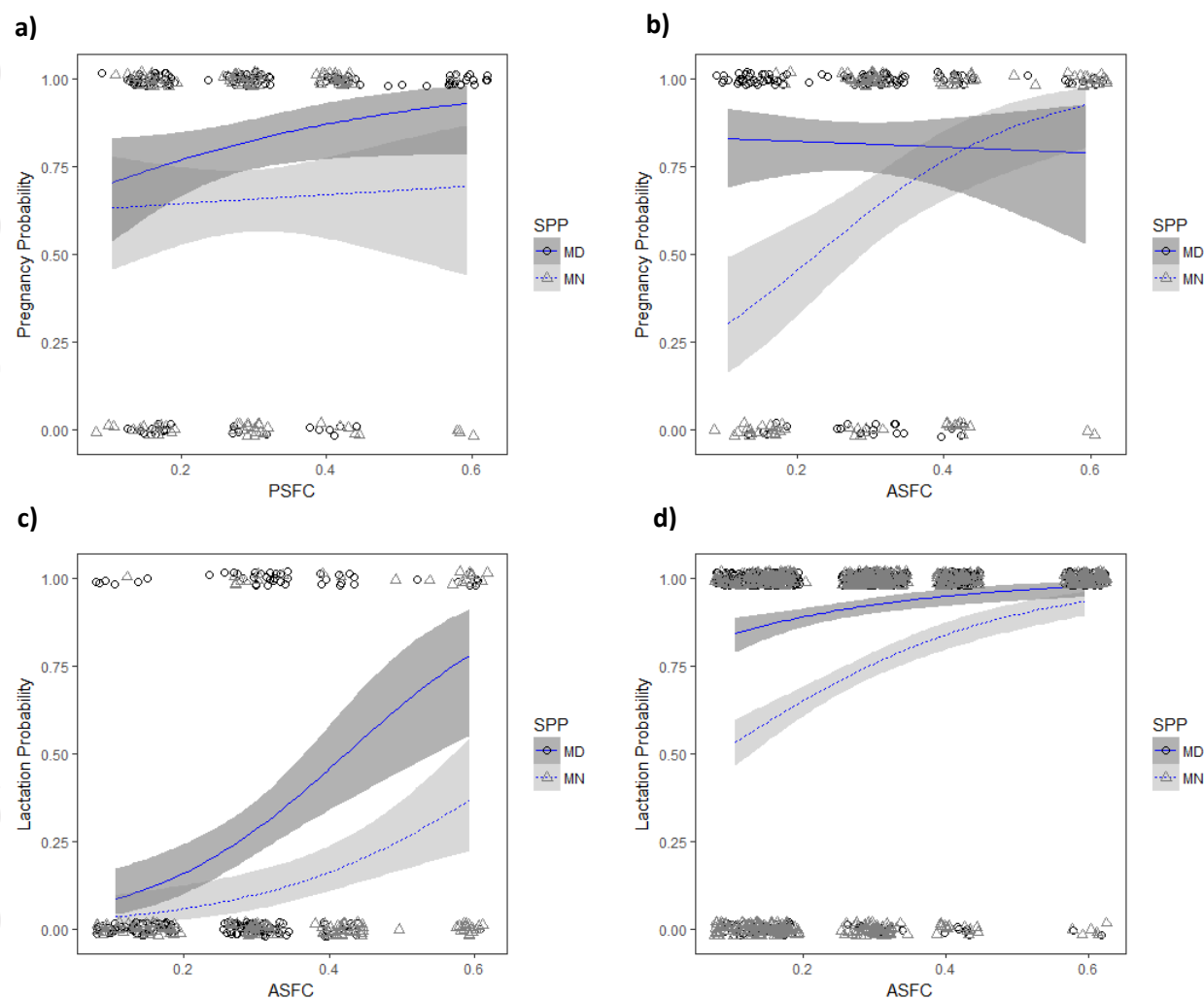


Figure 4

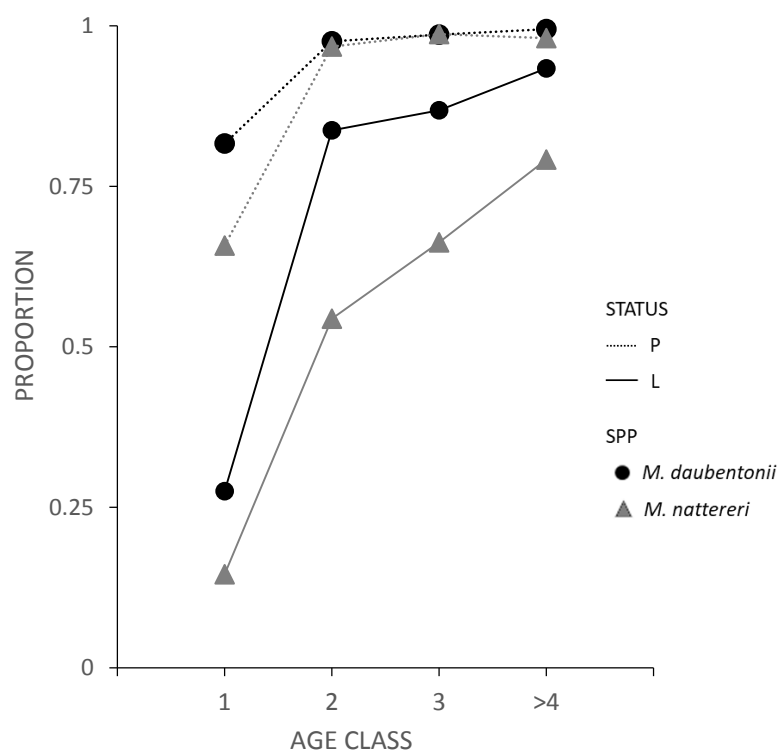


Figure 5

