

Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*

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Summary

1. Estimating variation in demographic rates, such as survival and fecundity, is important for testing life-history theory and identifying conservation and management goals.

2. We used 16 years (1993–2008) of mark–recapture data to estimate age-specific survival and breeding probabilities of the little brown myotis *Myotis lucifugus* LeConte in southern New Hampshire, USA. Using Kendall & Nichols' (1995) full-likelihood approach of the robust design to account for temporary emigration, we tested whether survival and breeding propensity is influenced by regional weather patterns and timing of reproduction.

3. Our results demonstrate that adult female survival of *M. lucifugus* ranged from 0.63 (95% CL = 0.56, 0.68) to 0.90 (95% CL = 0.77, 0.94), and was highest in wet years with high cumulative summer precipitation. First-year survival [range: 0.23 (95% CL = 0.14, 0.35) to 0.46 (95% CL = 0.34, 0.57)] was considerably lower than adult survival and depended on pup date of birth, such that young born earlier in the summer (*c.* late May) had a significantly higher probability of surviving their first year than young born later in the summer (*c.* mid-July). Similarly, the probability of young females returning to the maternity colony to breed in the summer following their birth year was higher for individuals born earlier in the summer [range: 0.23 (95% CL = 0.08, 0.50) to 0.53 (95% CL = 0.30, 0.75)].

4. The positive influence of early parturition on 1st-year survival and breeding propensity demonstrates significant fitness benefits to reproductive timing in this temperate insectivorous bat.

5. Climatic factors can have important consequences for population dynamics of temperate bats, which may be negatively affected by summer drying patterns associated with global climate change.

6. Understanding long-term demographic trends will be important in the face of a novel disease phenomenon (White-Nose Syndrome) that is associated with massive mortalities in hibernating bat species, including *M. lucifugus*, in the northeastern United States.

Key-words: breeding probability, capture–recapture, climate change, robust design

Introduction

Estimation of demographic rates is not only of fundamental interest to life-history theory and population ecology, but can also be critically important for successful conservation and management of species. Long-term, baseline demographic information can be particularly useful for evaluating potential population-level impacts of novel threats, such as emergent diseases, sudden loss or degradation of habitats, or future climate change (Lebreton *et al.* 1992; Morris & Doak 2002; Grosbois *et al.* 2008). Concern about ecological impacts of global climate change has raised interest in how

demographic parameters, such as survival and fecundity, may be influenced by climatic conditions (Saether *et al.* 2000; Stenseth & Mysterud 2002; Winkler, Dunn & McCulloch 2002; Ludwig *et al.* 2006; Jouvrier *et al.* 2009). Long-term mark–recapture datasets are costly to procure and are therefore rare, yet such datasets provide extraordinary opportunities to estimate vital rates and to test hypotheses about how climatic factors can influence such rates (Grosbois *et al.* 2008).

Bats are the second-most diverse group of mammals and provide important ecosystem services in terms of insect suppression, pollination and seed dispersal (Jones *et al.* 2009). Bats have unusual life history strategies for their size; they are generally long-lived (*c.* 20–30 years) and typically have

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small litters of 1–2 pups per annum (Wilkinson & South 2002; Barclay & Harder 2003). Reduced litter size and lower mortality risks may be influenced by their ability to fly (Pomeroy 1990; Haysen & Kunz 1996; Barclay & Harder 2003). Hibernation may also contribute to increased longevity in bats, by reducing senescence due to long periods of inactivity and increasing over-winter survival (Wilkinson & South 2002). In many temperate bat species, maternity colonies form in the spring after emergence from hibernation for synchronized birthing and rearing of young. Selection should favour parturition early in late spring/early summer to provide time for young to learn to forage successfully and establish adequate fat stores before winter, as depositing adequate fat is critical for over-winter survival for hibernating species (Ransome 1989; Thomas, Dorais & Bergeron 1990; Kunz, Wrazen & Burnett 1998). In addition, selection should favour matching high energetic demands of lactation to coincide with greatest seasonal resource availability (Visser *et al.* 1998).

Although general life-history trends are known, there are few quantitative estimates of demographic rates for bat species (O'Shea, Ellison & Stanley 2004; Frick, Rainey & Pierson 2007; O'Donnell 2009). Quantitative data on reproductive rates are equally scarce (Barclay *et al.* 2004). Given that 51% of microchiropteran bats are listed as either critically endangered, endangered, data-deficient, vulnerable, or near threatened (Hutson, Mickleburgh & Racey 2001), a better understanding of survival and reproductive rates of bat populations is important for conservation and management (Racey & Entwistle 2003). In particular, analysis of demographics of temperate insectivorous bats in North America is needed in the face of White-Nose Syndrome (WNS), an emerging disease phenomenon responsible for mortality rates greater than 75% at hibernacula for several species in the northeastern U.S. (Blehert *et al.* 2008).

Recent statistical approaches allow estimation of survival and temporary emigration from capture-recapture data if auxiliary data, such as multiple recapture events within a season, are available (Pollock 1982; Kendall & Nichols 1995; Kendall, Nichols & Hines 1997; Schwarz & Stobo 1997). For animal populations that are marked each year at breeding sites, temporary emigration (γ'') can be interpreted as probability of breeding ($1-\gamma''$), if non-reproductive animals do not return to the breeding site in a given year (Kendall & Nichols 1995). Colonially breeding animals, such as bats, are well-suited to this approach (Kendall & Nichols 1995; Sedinger, Lindberg & Chelgren 2001; Sandercock 2006). To our knowledge, no previous studies have attempted to simultaneously estimate annual survival and temporary emigration for colonial bat populations (O'Shea *et al.* 2004). Fidelity to maternity colonies is unusually high (Lewis 1995), but if temporary emigration occurs, then mark-recapture studies at bat maternity colonies could underestimate capture probabilities and produce biased survival estimates (Kendall *et al.* 1997). Estimation of temporary emigration also provides valuable data on reproductive rates, helping quantify important population parameters.

We use 16 years (1993–2008) of mark-recapture data from a maternity colony of little brown myotis *Myotis lucifugus* LeConte in southern New Hampshire to estimate annual survival and breeding probabilities. We empirically test hypotheses about the influence of climatic conditions on annual survival and breeding and quantify age-specific differences in these parameters. Understanding the importance of variation in weather patterns on demographic rates may help predict how future climate changes in the northeastern U.S. could affect bat population stability. Like many insectivorous passerines, bats depend on the synchronicity of insect prey reaching peak densities during the energetically high demands of the summer reproductive season (Anthony, Stack & Kunz 1981; Jones, Doran & Holmes 2003). Changes in weather patterns that influence prey availability during the summer and fall months could have significant consequences for survival and reproductive success for bats (Rodenhouse *et al.* 2009). In addition, our study quantitatively determines potential fitness benefits from timing of parturition (Ransome 1989; Ransome & McOwat 1994; Arlettaz *et al.* 2001) by assessing the influence of pup date of birth on first year survival and breeding propensity.

Materials and methods

DATA COLLECTION

We captured adult female bats at a maternity colony located in a barn structure in Peterborough, New Hampshire during 16 summer seasons (1993–2008). Capture events occurred between early May and mid August and ranged from 5 to 26 visits per summer. Bats were captured in their roost between 05.00 h and 07.00 h and marked with a lipped aluminium forearm band (Porzana Limited, East Sussex, UK, Kunz & Weise 2009). This type of band is the most reliable for bats, but some band loss did occur (< 3% over the 16 year study period), which could negatively bias our estimates (Keen 1988; Kendall 2008). Bats were aged as young-of-the-year or adult (≥ 1 year-olds) based on ossification of the fourth metacarpal joint (Brunet-Rossinni & Wilkinson 2009). Date of birth of young-of-the-year was estimated using equations for length of forearm and total length of epiphyseal gap in the fourth metacarpal joint and then subtracting estimated age at capture from date of capture (Kunz & Anthony 1982). Young males were excluded from analysis because they permanently emigrate from their natal roost (Reynolds 1999). Reproductive condition of adults was classified as pregnant, lactating, or post-lactating based on palpitation of the abdomen and nipple condition (Racey 2009).

HYPOTHESES AND PREDICTIONS

We predicted that 1st year survival would be lower than adult survival in *M. lucifugus*, as age-specific differences in mortality risks have been noted in other temperate bats (Sendor & Simon 2003; Pryde, O'Donnell & Barker 2005; Ellison *et al.* 2007; Frick *et al.* 2007). Theory predicts that young bats born earlier in the summer should have higher chances of survival because they will have more time to learn to forage efficiently and store fat before hibernation (Ransome 1989). We used pup date of birth as an individual covariate on 1st year survival to determine whether young born earlier in the year would have increased survival. We also predicted age-specific differences in breeding probabilities. Because bats cannot

be aged after their first winter, there are very few estimates of age-to-first-breeding or age-specific variation in reproductive rates (Barclay *et al.* 2004). We modelled age-specific differences in temporary emigration (γ'') and used pup date of birth as an individual covariate based on the probability of bats returning to the maternity colony in the summer following their birth year. We predicted that individual pups born earlier in the year would have a higher probability of breeding the following summer because of increased likelihood of sexual maturity during the fall mating period.

We used daily weather records (NOAA Online Climate Data Directory) from the closest reliable weather station at Concord, New Hampshire (<75 km from the study site) to represent regional climate. We calculated three different climatic variables (cumulative precipitation, average minimum daily temperature, and drought severity index) over two seasonal periods (active season from April to October and hibernating season from November to March). We predicted that variation in average minimum temperature could be an important influence on bat survival during the active season as temperature is known to influence insect abundance and activity and bat foraging activity (Anthony *et al.* 1981). We hypothesized that variation in precipitation may also influence bat survival if insect prey abundance is higher in wet years, as has been found for some insectivorous passerines in New Hampshire (Sillett, Holmes & Sherry 2000). We used a drought severity index (the Palmer Modified Drought Index) to test the joint effects of temperature and precipitation on bat survival. We predicted that weather conditions from April to October would have the strongest influence on bat survival, as this is the period when bats are active and foraging. For drought severity, we used annual average values because summer and winter indices were highly correlated. To test if fall weather during the fattening period prior to hibernation influences survival, we calculated a fall severity index as the number of days in August–October when minimum daily temperature was < 10 °C, a critical threshold below which insects are inactive and bat foraging is greatly reduced (Anthony *et al.* 1981; Ciechanowski *et al.* 2007). We used a similar index of spring severity to test whether spring weather (March–May) influenced the probability of females returning to the maternity colony ($1-\gamma''$).

DATA ANALYSIS

We used the full-likelihood approach of the closed robust design, which combines open and closed capture-recapture models to estimate annual apparent survival (S), temporary emigration (γ), encounter rate (p), and population size (N) (Kendall *et al.* 1997; Kendall 2008). We modelled main effects of constant survival S(.), age-dependent (young vs. adult) survival S (ya), six weather covariate-dependent models [S (summer precipitation), S (winter precipitation), S (summer temperature), S (winter temperature), S (annual drought severity index) and S (fall severity), and an individual covariate of pup date of birth on first-year survival S (young-dob)]. We combined main, additive and interactive effects of these variables, resulting in 27 a priori models for survival (Appendix S1).

Temporary emigration is represented by two different parameters, γ''_i and γ'_i (Kendall *et al.* 1997; Kendall 2008). Parameter γ''_i is the probability that a bat present in the colony at time i leaves the colony and does not return and is thus unavailable for encounter in time $i + 1$. Parameter γ'_i represents the probability that a bat not present in the colony at time i returns and is available for encounter in time $i + 1$. We tested nine different models of temporary emigration, including models of no movement, random and Markovian constant temporary emigration, age-specific models, weather-depen-

dent (spring severity) models, and an individual covariate of pup date of birth on probability of temporary emigration of one-year olds (Appendix S1).

We pooled all capture events (5–26 per year) into two secondary encounter occasions per primary sampling period because of low recapture rates and to reduce the number of parameters in each model (W.L. Kendall, pers. comm.). Given the nature of our capture conditions, we did not expect any trap dependence, but did expect temporal variability in recapture. We modelled time dependence on recapture (M_t) as well as an index of the number of capture events pooled into each recapture occasion as a covariate of capture effort.

The closed robust design assumes that the population is demographically closed during the primary period (i.e. between secondary sampling sessions) and that survival is the same for individuals inside and outside the sampling area (Kendall *et al.* 1997). We tested for the assumption of closure using Program CloseTest (Stanley & Burnham 1999) using a modified data set with sampling events pooled into 3–6 encounter occasions (Stanley & Burnham 1999). We used an omnibus goodness-of-fit test using RDSURVIV to test the fit of the data and estimate the variance inflation factor \hat{c} (Hines 1996). Predefined models in RDSURVIV do not account for age structure, so we used pre-defined model p(t,t), S(t), $\gamma(\cdot)$ as the global model and estimated \hat{c} by dividing Pearson's χ^2 by the degrees of freedom to adjust for overdispersion in our data (Hines 1996).

We used small-sample corrected Quasi-Akaike Information Criteria (QAICc), which accounts for over-dispersion, for model selection (Burnham & Anderson 2002). We used Akaike weights, w_i , to measure relative support of the data for any given model (Burnham & Anderson 2002). All analyses were conducted in RMark (Laake & Rexstad 2008), a newly developed package for program R (R Development Core Team 2007) that uses custom scripts to call program MARK (White & Burnham 1999).

Results

During the 16-year study period, we captured and marked 2891 female *M. lucifugus* (1295 young, 1596 adults) (Table 1). The proportion of female young to adults captured each year averaged 29%, but was unusually high in 2004 when 53% of animals captured were female young-of-the-year. Reproductive rate (proportion of adult females in reproductive condition) was high in all years (range: 92–99%) except in 2008 when it fell to 87% (Table 1).

GOODNESS OF FIT AND CLOSURE

The goodness-of-fit test from program RDSURVIV indicated a reasonable fit to a general model and our estimate of the variance inflation factor ($\hat{c} = 1.9$) indicated some overdispersion in the data. Overdispersion is likely due to heterogeneity caused by differences in age structure, which were accounted for in our final model set. We used QAICc, adjusted by $\hat{c} = 1.9$, to account for overdispersion in our results for model selection and report adjusted standard errors. The assumption of closure at the maternity colony during the sampling period from May to August was supported by our results of the test for closure in all years except 1996 (Appendix S2).

Table 1. Number of *Myotis lucifugus* captured each year (1993–2008). Reproductive rate equals the proportion of adults in breeding condition. Totals for each year include individuals captured in multiple years. Individually marked animals totalled 2891 (1295 young and 1596 adults)

Year	Adults			Young	Total
	Breeding	Non-breeding	Reproductive rate		
1993	218	19	0.92	128	365
1994	349	17	0.95	150	516
1995	229	16	0.93	98	343
1996	312	18	0.95	101	431
1997	136	7	0.95	57	200
1998	210	6	0.97	52	268
1999	188	1	0.99	48	237
2000	170	7	0.96	46	223
2001	144	1	0.99	59	204
2002	191	12	0.94	54	257
2003	178	7	0.96	87	272
2004	105	6	0.95	125	236
2005	161	9	0.95	100	270
2006	164	7	0.96	54	225
2007	107	3	0.97	65	175
2008	129	19	0.87	71	219
Grand totals	2991	155	0.95	1295	4441

MODEL SELECTION

Results of model selection indicated strong support for a best-fit model (57% of QAIC_c weights; Table 2) that incorporated the individual covariate of pup date of birth on 1st year survival and summer precipitation as a time-varying covariate on adult survival. This top model also incorporated pup date of birth as an individual covariate on the probability of young returning to the maternity colony in the year following their birth (1- γ) and probability of temporary emigration of adults fixed at zero. For compari-

son, the penultimate model had only 13% of the support of the data based on QAIC_c weights (Δ QAIC_c = 2.88) and was similar to the best-fit model except 1st year survival was dependent on summer precipitation instead of pup date of birth. These two models shared the same model structure for temporary emigration, demonstrating strong support (70% of model weights) for the influence of date of birth on the probability of bats returning to the maternity colony in the year following their birth and no temporary emigration of adults (Table 2). Summer precipitation was the only weather covariate tested that had any support from the data. Model selection indicated strong support for time dependence in recapture (99.9% of QAIC_c weights) and no support for a covariate of effort on recapture. We present parameter estimates from the best-fit model below.

PARAMETER ESTIMATES

First-year survival of female *M. lucifugus* at our study site was variable, ranging from 0.23 (95% CL = 0.14, 0.35) to 0.46 (95% CL = 0.34, 0.57) and depended on pup date of birth, such that bats that were born earlier in the summer (*c.* late May–early June) had higher survival rates than individuals born later in the summer (*c.* mid-July) (Fig. 1). The slope coefficient for the influence of Julian date of birth on 1st year survival was estimated (mean \pm SE) at -0.018 ± 0.008 (95% CL = $-0.03, -0.002$) on a logit scale. Adult survival was considerably higher than 1st year survival and ranged from 0.63 (95% CL = 0.56, 0.68) to 0.90 (95% CL = 0.77, 0.94), depending on amount of cumulative precipitation from April to October (Fig. 2). The slope coefficient for the influence of cumulative summer precipitation on adult annual survival was estimated at 0.07 ± 0.018 (95% CL = 0.04, 0.11) on a logit scale, suggesting that wet years with higher levels of precipitation are associated with higher survival.

The best-fit model in our analysis indicates that adult females do not skip breeding by not returning to the

Table 2. Summary of the top 10 models from model selection results. Models are ranked by ascending Δ QAIC_c

Model	QAIC _c	Δ QAIC _c	QAIC _c weights	Parameters
S[adult(sum.precip.),young(dob)], γ [young(dob), adult(0)] = $\gamma'(0)$	-10 341.45	0	0.57	70
S(ya + sum.precip), γ [young(dob), adult(0)] = $\gamma'(0)$	-10 338.57	2.88	0.13	69
S[adult(sum.precip.),young(dob)], γ [young(dob), adult(spr.severity)] = $\gamma'(spr.severity)$	-10 337.63	3.82	0.08	74
S(ya * sum.precip), γ [young(dob), adult(0)] = $\gamma'(0)$	-10 336.99	4.46	0.06	70
S[adult(sum.precip.),young(dob)], γ [young(.), adult(0)] = $\gamma'(0)$	-10 336.64	4.81	0.05	69
S[adult(sum.precip.),young(dob)], γ [young(spr.severity), adult(0)] = $\gamma'(0)$	-10 334.77	6.68	0.02	70
S[adult(sum.precip.),young(dob)], $\gamma' = \gamma'(ya)$	-10 334.58	6.87	0.02	70
S(ya + sum.precip), γ [young(dob), adult(spr.severity)] = $\gamma'(spr.severity)$	-10 334.42	7.03	0.02	73
S(ya * sum.precip), γ [young(dob), adult(spr.severity)] = $\gamma'(spr.severity)$	-10 333.00	8.45	0.01	74
S(ya + sum.precip), γ [young(.), adult(0)] = $\gamma'(0)$	-10 332.71	8.74	0.01	71

All models shown had time-dependence on recapture [$p(t) = c(t)$].

Model notation: dob = date of birth; spr.severity = number of days when minimum daily temperature < 10 °C from March to May; sum.precip = cumulative precipitation from April to October; ya = two age groups: young (1st year) and adults; (0) = parameter fixed at zero; * = interactive effects; + = additive effects. See Appendix S1 for more details on model nomenclature.

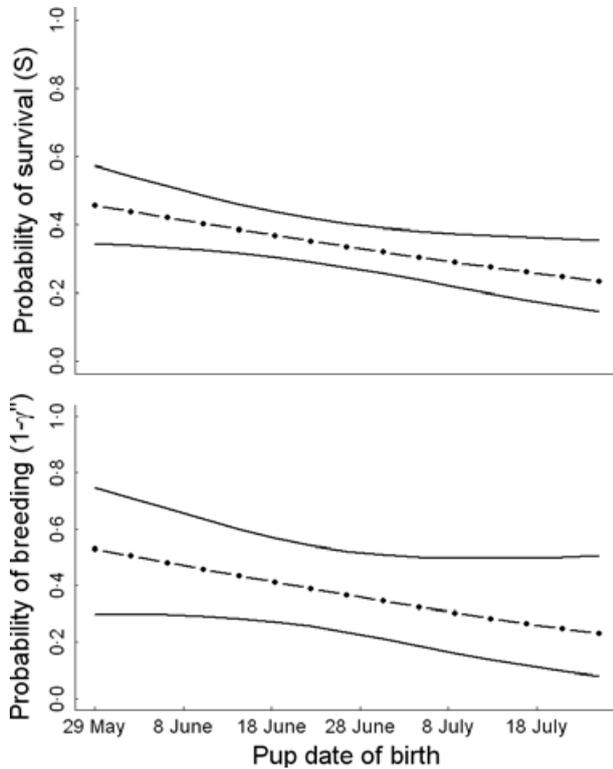


Fig. 1. Relationship of probability of survival (S) (top panel) and probability of breeding ($1-\gamma''$) (bottom panel) and date of birth for 1st-year *Myotis lucifugus* in southern New Hampshire.

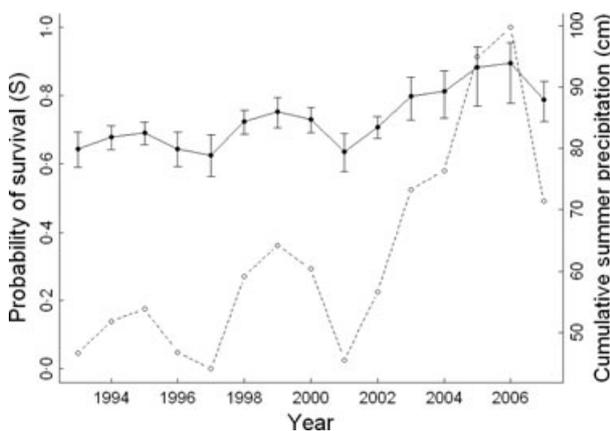


Fig. 2. Apparent annual survival estimates from 1993 to 2008 of adult female *Myotis lucifugus* in southern New Hampshire (filled circles; solid line). Adult survival varied by amount of cumulative summer precipitation (open circles; dashed line).

maternity colony (e.g. temporary emigration was fixed at 0). In contrast, probability of breeding ($1-\gamma''$) was variable for 1st year bats, ranging from 0.23 (95% CL = 0.08, 0.50) to 0.53 (95% CL = 0.30, 0.75), depending on an individual's date of birth (Fig. 1). The slope coefficient for the influence of Julian date of birth on 1st year temporary emigration (γ'') was estimated at 0.02 ± 0.016 (95% CL = $-0.008, 0.06$) on a logit scale, suggesting that individuals born earlier in the summer have a higher probability of returning to the

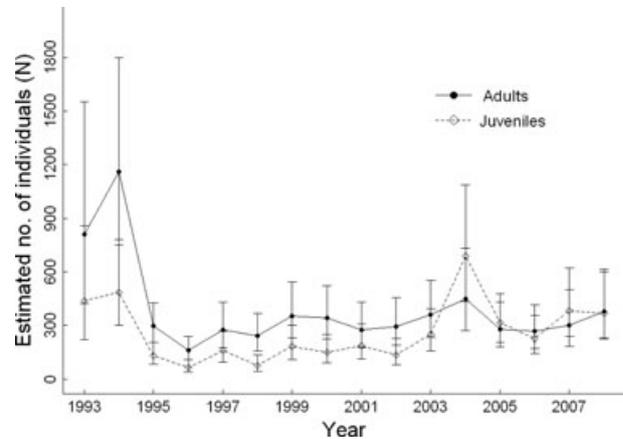


Fig. 3. Annual estimates of colony size of *Myotis lucifugus* at the Carr barn, Peterborough, New Hampshire, indicating number of adults (solid line and filled circles) and juveniles (dashed line and open diagonals).

maternity colony in the summer following their birth than those born later in the summer.

Recapture rates were low and generally ranged from 0.10 to 0.35 over the 32 encounter occasions (2 per year for 16 years). There was one occasion in 1996 with a recapture probability of 0.47 (95% CL = 0.38, 0.56) and five occasions with recapture rates < 0.10 (years: 1994, 1997, 1999, 2004 and 2007).

Estimates of colony size declined steeply after the first two seasons, but were roughly stable from 1995 to 2008 (Fig. 3). In general, the juvenile population was approximately half the size of the adult population, which was expected given that females give birth to a single pup each year and males were excluded from the analysis. In 2004, the estimate of number of juveniles was greater than the number of adults and this may be due to some heterogeneity in recapture. In this same year, the proportion of juveniles to adults captured was unusually high at 53%, whereas in most years the proportion of captured juveniles to adults ranged from 0.19 to 0.37 (Table 1).

Discussion

This study demonstrates that climatic conditions are correlated with annual survival of adult female *M. lucifugus* and that timing of parturition has strong fitness consequences in terms of 1st year survival and age to first breeding. Our estimates of adult annual survival ranged from 0.63 to 0.90 and are consistent with known survival rates for temperate insectivorous bats (Keen & Hitchcock 1980; Hitchcock, Keen & Kurta 1984; Sendor & Simon 2003; Pryde *et al.* 2005; Boyles *et al.* 2007; Ellison *et al.* 2007; Frick *et al.* 2007; Federico, Dimitrov & McCracken 2008). Life-history theory predicts survival in bats should be high, given their low fecundity and long life spans (Barclay & Harder 2003). Although adult survival rates in this study were fairly high, estimates of 1st year survival were considerably lower (range: 0.23–0.46) than we

expected based on other studies of myotid bats (Frick *et al.* 2007). The influence of pup date of birth on 1st year survival and breeding propensity provides one of the first quantitative assessments of fitness consequences to timing of parturition in bats (Ransome 1989).

INFLUENCE OF CLIMATE ON ANNUAL SURVIVAL

Climate likely influences survival and reproduction in temperate insectivorous bats by controlling productivity of insects and thus food availability during the energetically demanding period of reproduction (Ransome & McOwat 1994; Sillett *et al.* 2000; Arlettaz *et al.* 2001). Many temperate vertebrates depend on the productivity of the temperate summer to meet energetic demands of reproduction as well as to store fat for over-winter survival. Insectivorous passerines in the northeastern U.S. show similar patterns of higher survival and reproductive success in wet years because of increased prey availability of lepidopteran larvae (Sillett *et al.* 2000). Although minimum temperature is most often associated with limiting volant insect availability and foraging activity of bats (Anthony *et al.* 1981; Ciechanowski *et al.* 2007), our results suggest that cumulative precipitation during the period of bat activity (April–October) is more strongly associated with annual survival. Lack of support for an influence of average minimum temperature on bat survival could be due to low year-to-year variability in temperature compared to that of seasonal precipitation (Hayhoe *et al.* 2007).

The link between moisture availability and insect abundance is the likely driver of the positive influence of summer precipitation on survival of *M. lucifugus*. High precipitation is associated with increased abundance of insects, including culicids (mosquitos), dipterans (flies), and lepidopterans (moths) (Williams 1951; Sillett *et al.* 2000; Landesman *et al.* 2007), which are important components in diets of this species in the northeastern U.S. (Anthony & Kunz 1977). Although foraging generalists, *M. lucifugus* forage heavily on aquatic emergent insects (Anthony & Kunz 1977; Syme, Fenton & Zigouris 2001). Diet selectivity may increase when insect abundance is high, suggesting that favourable climatic conditions could increase prey quality as well as quantity (Anthony & Kunz 1977). The positive influence of precipitation on survival may be regionally variable and depend on timing of precipitation (Grindal, Collard & Brigham 1992; Syme *et al.* 2001; Burles *et al.* 2009).

Climate change will likely influence wildlife populations in complex ways, such as altering food availability and timing of reproduction as well as disrupting the synchronicity of prey availability during physiological stressful periods (Rodenhouse *et al.* 2009). Projections of changes in regional climate in the northeast indicate that winter precipitation will increase but summer precipitation will decrease slightly, and summers may be drier due to rising temperatures and lengthening of the growing season, creating longer periods of drought (Hayhoe *et al.* 2007, 2008; Huntington *et al.* 2009). These regional climatic changes could have profound influ-

ences on bat populations in the northeastern U.S., especially if increased summer drying affects the availability of insect prey during reproduction (Rodenhouse *et al.* 2009). Populations of *M. lucifugus* in the northeastern U.S. could be negatively affected by drying summer conditions associated with climate change as annual survival of adult females is reduced in drier years (Fig. 2). Population growth in long-lived species is often sensitive to variation in adult survival relative to other fitness components, and therefore results of this study raise important considerations for conservation of this species (Gaillard *et al.* 2000). Future studies on how projected climate change will influence abundance and temporal availability of insects are needed to better understand the causal relationships between climate and bat survival (Rodenhouse *et al.* 2009).

FITNESS CONSEQUENCES OF TIMING OF PARTURITION

Our results suggest early parturition has significant fitness benefits, given that young born in early summer have a higher probability of surviving and breeding in their first year than pups born later in the summer (Fig. 1). Young bats need time to learn how to forage successfully and deposit fat stores prior to hibernation. Selective pressures should favour early parturition, as differences of just a few weeks result in significant differences on a young bat's chance of survival and reproducing. This is consistent with predictions from life-history theory and work by Ransome (1989) and Hoying & Kunz (1998) that showed late parturition had negative consequences for growth and survival of juvenile greater horseshoe bats *Rhinolophus ferrumequinum* in Great Britain, and tricoloured bats *Perimyotis subulatus* in Massachusetts, respectively. Other studies have shown that food availability and weather conditions may influence the timing of parturition in insectivorous bats (Racey 1973; Grindal *et al.* 1992; Arlettaz *et al.* 2001; Burles *et al.* 2009). Our work emphasizes how reproductive timing and factors that influence when young are born have important consequences for population dynamics of this species by influencing 1st year survival and breeding propensity.

Our estimates of 1st year survival were lower than other estimates for temperate bat species (Sendor & Simon 2003; Pryde *et al.* 2005; Ellison *et al.* 2007; Frick *et al.* 2007). Age-specific survival has been reported in several bat populations and adult survival tends to be significantly higher than 1st year survival (Hoyle, Pople & Toop 2001; Sendor & Simon 2003; Pryde *et al.* 2005; Ellison *et al.* 2007; Frick *et al.* 2007). The robust design directly accounts for temporary movement away from the maternity colony by estimating temporary emigration, but permanent emigration from the natal roost could negatively bias survival (Kendall *et al.* 1997). Confounding of permanent emigration and mortality is a common problem in mark-recapture studies (Sandercock 2006). Some band loss occurred over the 16-year study period and may have been more problematic for young bats (D.S. Reynolds, pers. obs), which could negatively bias survival estimates. Mortality risks for 1st year bats could also be

higher in our study area than in other populations and regional variability in mortality could be important for understanding spatial population dynamics (Pulliam 1988).

REPRODUCTIVE RATES

Reproductive rates within the maternity colony were markedly high (Table 1). Over the 16-year study period, an average of only 5% of adult females captured in the maternity colony were in non-reproductive condition (Table 1). This contrasts with Barclay *et al.*'s (2004) prediction that high survival rates should provide flexibility to forgo breeding if conditions are unfavourable. Measuring reproductive rates (proportion of breeding to non-breeding females) at maternity colonies may be positively biased if non-reproductive females do not return to the maternity colony in years when they forgo breeding (Barclay *et al.* 2004). Females who are reproductively active benefit from the thermodynamic and social advantages conferred by colonial behaviour during pregnancy and lactation, but these benefits may not attract non-reproductive females (Barclay *et al.* 2004). Our data suggest this may be true for 1 yr old females, who have a 23–53% probability of returning to the colony to breed in the summer after their birth year. However, our data indicate that adult females return to the colony each year regardless of their breeding status, as the best-fit models fixed the probability of an adult bat leaving the colony for a given year at zero (Table 2). This suggests that proportions of breeding to non-breeding females found in maternity colonies should be representative of the adult population's reproductive rate.

In 2008, the reproductive rate at this colony was notably lower than the previous 15 years (Table 1). This reduction could be related to the recent spread of White-Nose Syndrome (WNS) into bats in the northeastern U.S. (Blehert *et al.* 2008). White-Nose Syndrome, named for the fungus (*Geomyces destructans*) that grows on muzzles and wings of hibernating bats, was first detected in caves in winter of 2006 in upstate New York and has been associated with altered hibernating behaviour and massive mortalities in hibernating caves throughout the northeastern U.S. (Blehert *et al.* 2008; Gargas *et al.* 2009). Our data suggest that in addition to high mortality at hibernacula, WNS could have other negative demographic effects by lowering reproductive rates of survivors, further impacting populations. Thus, further research is urgently needed to assess reproductive rates of *M. lucifugus* in the northeastern U.S. since the appearance of WNS, so that these data can be compared.

POPULATION TRENDS

Estimates of colony size from our analysis suggest there was a significant decline in number of individuals at the maternity colony after the first two years of the study, but that the population was relatively stable from 1995 through 2008 (Fig. 3). The cause of the population decline in 1995 is not clear, but could be due to a variety of factors, including disturbance to the colony due to the installation of a new roof on the barn.

For most years, estimates of the number of female juveniles are roughly half the number of female adults, which is what we would expect if sex ratios of young are close to 1:1, given that females give birth to one pup per year and males were excluded from the analysis. However, in the later years of the study, there are unexpected patterns of higher estimates of female juveniles than adults. Heterogeneity in recapture among adults and juveniles in 2004–2008 is the most parsimonious explanation and corresponds to a shift in sampling effort concentrated later in the maternity season.

Monitoring of summer maternity colonies may prove important for determining population-level impacts of White-Nose Syndrome on northeastern bat populations. An estimated 1 million bats have died since 2007, when mortalities were first observed (A. Hicks, unpublished data). White-Nose Syndrome has rapidly spread geographically each winter and reached as far south as Virginia in 2008–2009, raising concerns about the population viability of this and other hibernating bat species. Mark-recapture studies at hibernacula are strongly discouraged because of potential negative impacts of disturbance to hibernating bats (Tuttle & Stevenson 1982), but summer maternity colonies could provide valuable data on regional population declines. The baseline data collected at this colony provides a long-term perspective on demographic and population trends for the most common species affected by this emerging disease.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Model structure for 27 a priori candidate models on survival (S) and nine models on temporary emigration parameters (γ'' and γ'). Model notation follows Kendall (2008), Lebreton *et al.* (1992), and Laake & Rexstad (2008)

Appendix S2. Results of closure tests for each year of the study using Stanley & Burnham (1999). Program CloseTest uses a null model of time dependence in capture probability, making it the appropriate test for closure for our data, given we expected temporal variation in capture probabilities.

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