


Live fast, don't die young: Survival–reproduction trade-offs in long-lived income breeders

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Abstract

1. Trade-offs between survival and reproduction are at the core of life-history theory, and essential to understanding the evolution of reproductive tactics as well as population dynamics and stability. Factors influencing these trade-offs are multiple and often addressed in isolation. Further problems arise as reproductive states and survival in wild populations are estimated based on imperfect and potentially biased observation processes, which might lead to flawed conclusions.
2. In this study, we aimed at elucidating trade-offs between current reproduction (both pregnancy and lactation), survival and future reproduction, including the specific costs of first reproduction, in long-lived, income breeding small mammals, an under-studied group.
3. We developed a novel statistical framework that encapsulates the breeding life cycle of females, and accounts for incomplete information on female pregnancy and lactation and imperfect and biased recapture rates. We applied this framework to longitudinal data on two sympatric, closely related bat species (*Myotis daubentonii* and *M. nattereri*).
4. We revealed the existence of several, to our knowledge previously unknown, trends in survival and breeding of these closely related, sympatric species and detected remarkable differences in their age and costs of first reproduction, as well as their survival–reproduction trade-offs.
5. Our results indicate that species with this type of life history exhibit a mixture of patterns expected for long-lived and short-lived animals, and between income and capital breeders. Thus, we call for more studies to be conducted in similar study systems, increasing our ability to fully understand the evolutionary origin and fitness effects of trade-offs and senescence.

KEYWORDS

bats, Daubenton's bat, multi-event model, *Myotis daubentonii*, *Myotis nattereri*, Natterer's bat, survival–reproduction trade-offs

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1 | INTRODUCTION

Organisms have limited access to resources and therefore need to allocate their time, energy and nutrients between the processes and traits that enhance their fitness (Kirkwood, 1977; Willams, 1966). The resulting trade-offs between different fitness components are the central tenet of life-history theory (Stearns, 1992), and their existence is well supported by empirical work. Across taxa, experimental manipulation of reproductive effort has, for example, revealed that costs of reproduction lead to reduced survival (e.g. Boonekamp, Mulder, Salomons, Dijkstra, & Verhulst, 2014; Dijkstra et al., 1990; Koivula, Koskela, Mappes, & Oksanen, 2003; Maklakov et al., 2017). Such costs of reproduction can affect demography and population dynamics (Proaktor, Coulson, & Milner-Gulland, 2008; Stoelting, Gutiérrez, Kendall, & Peery, 2015). Moreover, they shape life-history trajectories, for example, by affecting the optimal onset of reproduction (e.g. Desprez et al., 2014; Mourocq et al., 2016) and/or the onset and rate of senescence (e.g. Bouwhuis, Charmantier, Verhulst, & Sheldon, 2010; Hammers, Richardson, Burke, & Komdeur, 2013; Lemaître & Gaillard, 2017; Nussey, Kruuk, Donald, Fowlie, & Clutton-Brock, 2006). In short-lived organisms (that have fast life-history tactics), trade-offs are expected to occur between current reproduction and survival, while in long-lived organisms (that have slow life-history tactics) they are expected to occur between current and future reproduction (Hamel et al., 2010).

Although costs of reproduction are assumed to generally be high (Hamel et al., 2010; Moyes et al., 2011), environmental conditions and individual quality may mitigate or exacerbate these costs (by altering the total energy available to an individual, Van Noordwijk & de Jong, 1986). For example, costs of reproduction can become visible only under harsh environmental conditions (e.g. Tavecchia et al., 2005). On the other hand, favourable environmental conditions may induce an increase in the relative allocation to reproduction and therefore an increase in the costs of reproduction (Erikstadt, Fauchald, Tveraa, & Steen, 1998). Moreover, individuals may not experience any costs of reproduction or the costs will vary with individual quality (e.g. Hamel, Côté, Gaillard, & Festa-Bianchet, 2009; Moyes et al., 2011; Zhang, Vedder, Becker, & Bouwhuis, 2015), age (e.g. Desprez et al., 2014; Hamel et al., 2010; Rughetti, Dematteis, Meneguz, & Festa-Bianchet, 2015) or natal cohort conditions (e.g. density, Nussey, Kruuk, Morris, & Clutton-Brock, 2007; food availability, Descamps, Boutin, Berteaux, & Gaillard, 2008; juvenile mortality, Garratt et al., 2015; but see Vedder & Bouwhuis, 2018). Elucidating factors that influence survival and reproduction, and the trade-off between the two, is challenging and requires multivariate analyses of long-term individual-based data, as only such studies have the potential to detect age-related variation in fitness components, as well as trade-offs and their dependence on age and environmental conditions (Clutton-Brock & Sheldon, 2010). Such studies will, however, need to account for detection and state-assignment issues (Hamel et al., 2010). This is because many studies suffer from imperfect (i.e. lower than one) and biased (i.e. consistently higher/lower for

a certain type of animals) detection (Gimenez et al. 2008) and inaccuracy in assigning reproductive status to individuals in wild populations (Culina, Lachish, Pradel, Choquet, & Sheldon, 2013), potentially leading to flawed conclusions.

Compared to most small mammals, bats are extremely long-lived and reproduce at low rates (Austad & Fischer, 1991; Turbill, Bieber, & Ruf, 2011; Wilkinson & South, 2002). This likely relates to their hibernating behaviour during winter (Turbill et al., 2011), which increases survival during the period of unfavourable foraging conditions. As most other small mammals, bats are income breeders (that largely rely on contemporary food sources, rather than stored fat reserves, during reproduction, Stephens, Boyd, McNamara, & Houston, 2009) and maintain high metabolic rates during pregnancy and lactation, when they have to produce around 25% of their body weight in milk each day (Henry, Thomas, Vaudry, & Carrier, 2002 and references therein). Reproduction in bats is demanding, especially during lactation, when energy (Rughetti & Toffoli, 2014; Swift, 1998) and food consumption (Encarnação & Dietz, 2006) are substantially elevated (placing them closer to the income breeder side of income-capital spectrum, Stephens et al., 2009). Reproduction has also been shown to lead to somatic deterioration: skeletal calcium deficiency develops during pregnancy and lactation (Kwiecinski, Krook, & Wimsatt, 1987), as does iron deficiency during lactation (Studier, Sevick, Keeler, & Schenck, 1994). Based on their longevity, low mortality and the known somatic costs of reproduction, bats are expected to exhibit delayed reproduction, senescence and reproductive trade-offs (similar to long-lived large mammals and birds, Bouwhuis, Choquet, Sheldon, & Verhulst, 2012; Hamel et al., 2010; Lemaître & Gaillard, 2017; Mourocq et al., 2016). On the other hand, high metabolic rates and income breeding could have led to less pronounced trade-offs between current and future reproduction (Hamel et al., 2010).

Although the life history of bats offers an intriguing system to test hypotheses on age-related reproduction and trade-offs, only a handful of studies have done so. These studies have provided mixed evidence for age-related patterns of female survival (improvement followed by senescence, Davis, 1966; no senescence, Fleicher et al. 2017; Greiner et al., 2014) and reproduction (improvement and no, or little senescence, Ward, Ransome, Jones, & Rossiter, 2014; improvement and no senescence, Fleicher et al. 2017; Greiner et al., 2014). To our knowledge, only one study investigated trade-offs and detected the existence of survival costs of breeding (Ransome, 1995). As such, the main aim of our study was to explore survival-reproduction trade-offs in long-lived, hibernating, income breeders.

Hereto, we use long-term individual-based data on two sympatric bat species, Daubenton's bat, *Myotis daubentonii*, and Natterer's bat, *M. nattereri*, to study age-specific performance and trade-offs between reproduction and survival and compare patterns between these two species. Both species hibernate in winter, typically produce a single offspring each year (Altringham, 2003) and adapt their reproductive cycles to seasonal fluctuations in prey availability (Encarnação & Dietz, 2006). The two species, however, show differences in their reproductive phenology (timing of pregnancy and

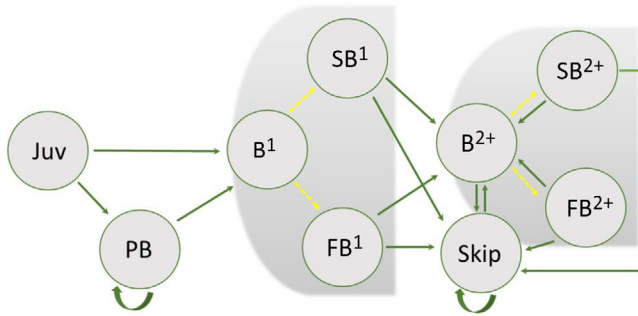


FIGURE 1 Schematic representation of the life cycle of female bats used to construct our modelling framework to study age-related reproduction, survival and trade-offs. Green arrows represent possible state transitions between consecutive breeding seasons. Yellow lines within the shaded areas represent transitions that occur within breeding seasons. Juvenile bats (Juv) and pre-breeders (PB) can either become or remain pre-breeders or become first-time breeders (B^1). B^1 can breed successfully (SB^1) or fail (FB^1), then become experienced breeders (B^{2+}) or skip breeding (Skip) in the following year. Experienced breeders (successful SB^{2+} or failed FB^{2+}) and skipped breeders can only transition amongst each other. All transitions are conditional on survival

lactation), feeding habits (see Methods) and hibernating behaviour (*M. nattereri* feeds during hibernation, Hope & Jones, 2012).

We develop a statistically rigorous framework that realistically describes the reproductive life cycle of females, while simultaneously incorporating uncertainty in the assessment of reproductive state and potentially biased recapture. We use this framework to explore (a) age-related patterns of survival and reproduction; (b) trade-offs between current reproduction (both pregnancy and lactation), survival and future reproduction, including the specific costs of first reproduction; (c) long- and short-term cohort effects; and (d) influences of weather variables on reproduction and costs of reproduction. Based on the bats' natural history, we predict several trends: (a) no delayed first reproduction and no age-specific costs of first reproduction. Bats generally attain their adult skeletal size by the end of their first spring (Kunz, Adams, & Hood, 2009) and become sexually mature during their first autumn (Kokurewicz & Bartmanska, 1992). Thus, we deem it unlikely that they face a trade-off between becoming breeders in their first year and completion of growth; (b) an increase in breeding success (i.e. success of lactation) with age as foraging ability might improve with experience (Hood, Bloss, & Kunz, 2002); and (c) reproduction is costly to over-winter survival but not to reproduction in the following year. Because bats are income breeders, reproduction (and especially lactation) should largely depend on the current food intake (rather than fat reserves). Reproduction, however, may cause females to allocate their current food intake in producing and feeding their young rather than in storing fat for themselves, such that females that reproduced are more likely to enter winter with lower fat reserves and suffer from reduced survival. Furthermore, we predict that lactation (as more energetically demanding and nearer to the onset of hibernation than pregnancy) is more costly to survival than pregnancy only (i.e. pregnancy that failed). However, because *M. nattereri* forages

during the hibernation period, this species might be able to avoid or mitigate the survival cost; (d) reproductive success (i.e. success of lactation) shows between-year fluctuations related to the quality of the breeding season; and (e) probability of pregnancy (which starts at the beginning of spring) depends on winter and/or spring conditions (female condition at the beginning of the breeding season will depend on the depletion of fat during hibernation).

2 | MATERIALS AND METHODS

2.1 | Data collection and study species

Data were collected in Wytham Woods, Oxfordshire, UK (51°77'N, 1°33'W), a 385 ha broadleaf deciduous forest surrounded by farmland. In these woods, bats roost in woodcrete nest-boxes provided and maintained by the Edward Grey Institute for monitoring of great and blue tit (*Parus major*, *Cyanistes caeruleus*) populations (Perrins & Gosler, 2010). Bats mainly take up residence in boxes in June (after the bird breeding season), but sometimes roost in boxes not used by birds prior to June. Between 2007 and 2015, boxes were checked for bat occupancy between March and October. However, 98% of captures occurred between May and September (see Supporting Information Table S1). Over 26,000 box checks resulted in 1,719 recorded bat roosts containing between 1 and 45 individuals in 751 boxes. When captured for the first time, females were marked with a unique ID tag (2.9 mm aluminium ring, under licence from SNCO) and aged as juveniles or adults, based on unfused or fused epiphyseal joints (Racey, 1974) and/or reproductive traits (pregnant or parous; adults). At each encounter, females were assigned to one of four categories: no signs of pregnancy, pregnant, lactating or post-lactating (see below).

We analysed data on 583 *M. daubentonii* and 474 *M. nattereri*, of which 305 and 313 females were captured more than once, with the average number of captures per female being 2.2 and 2.8, respectively. The numbers of females aged as juveniles when captured for the first time (and thus of known age) were 280 *M. daubentonii* and 203 *M. nattereri*. At temperate latitudes, the bat mating season occurs from autumn until spring, with both sexes storing sperm through winter hibernation (Altringham, 2011). The timing of ovulation and fertilization and the duration of the gestation period are influenced by spring weather conditions (Racey & Swift, 1981). In our study system, parturition typically occurs during late May to mid-June in *M. daubentonii* and 1–2 weeks later in *M. nattereri* (Linton & Macdonald, 2018). Juveniles become volant and are weaned at 5–6 weeks of age. *Myotis daubentonii* specialize in feeding over calm open water, while *M. nattereri* forage primarily in woodland, gleaning invertebrates from the surface of vegetation (Altringham, 2003).

2.2 | Life cycle states and modelling framework

To study age-related reproduction and survival, and reproductive trade-offs, while controlling for imperfect and potentially biased recapture rates and the uncertainty in the assessment of reproductive state, we constructed a model that describes the life cycle of

TABLE 1 Eight possible events (0–7) that were used to construct a female encounter history. Events are determined based on early and/or late observations of reproductive condition. Each event relates to one or more possible underlying state(s)

Early observation	Late observation	Event code	Possible state(s)
Captured pregnant or not captured	Captured, lactating	1	SB ¹ , SB ²⁺
Captured pregnant	Not captured (or unreliable)	2	FB ¹ , FB ²⁺ , SB ¹ , SB ²⁺
Captured pregnant	Captured, not lactating	3	FB ¹ , FB ²⁺
Not captured (or unreliable)	Captured, not lactating	4	PB, FB ¹ , FB ²⁺ , Skip
Captured, not pregnant	Captured, not lactating	5	PB, Skip
Contradictory information		6	Any live state
Captured as a juvenile		7	Juvenile
Not captured	Not captured	0	All states possible (including dead)

Note. PB = pre-breeder, SB¹ = successful first-time breeder, SB²⁺ = successful experienced breeder, FB¹ = failed first-time breeder, FB²⁺ = failed experienced breeder.

individuals based on multi-event capture–mark–recapture framework (Pradel, 2005). We describe the female life cycle using eight states: juvenile (Juv), pre-breeder (PB), skipped breeder (Skip), successful first-time breeder (SB¹), failed first-time breeder (FB¹), successful experienced breeder (SB²⁺), failed experienced breeder (FB²⁺) and dead (Figure 1). In the year in which a female is born, she is in the state Juv and, by default, non-breeding. In the following breeding season(s), the female can become a pre-breeder or a first-time breeder (B¹). In any subsequent breeding season, first-time breeders transition to being experienced breeders (B²⁺). Breeders can be either successful (lactating during the maternity period, SB) or fail (FB). When a female that has bred before (i.e. a parous adult) does not breed in the current season, she is in the state skipped breeder (Skip).

The reproductive state of a female is inferred from information collected at capture on (a) weight, (b) visual or physical examination to determine pregnancy and (c) inspection of nipple condition (nulliparous, lactating, post-lactating or parous non-breeding). However, depending on the timing and frequency of captures during the maternity period, this information relates with a different level of certainty to the true reproductive state of a female. For example, if a female is encountered while pregnant, but not at a later stage, she could be either a successful or a failed breeder. If a female is only seen in late autumn, then it is no longer possible to reliably distinguish between post-lactating breeders and parous non-breeders. Thus, based on breeding phenology, we divided our reproductive assessment data into early (pregnancy) and late (post-parturition) maternity periods and defined eight events (coded 0–7, Table 1) that relate field observations to the true reproductive state of females in a given breeding season. The capture history of each female consists of a series of event codes, one code per year (2007–2015).

To model survival and transition of females between states, and to relate the observations of females to the true underlying state, we used five probabilistic matrices: the first three matrices describe state transition of individuals between two subsequent

years ($t-1$ and t), while the second three matrices describe the observation process (captures and the assessment of the individual state in the year t). Details of the framework are given in the Supporting information. The first capture of an individual is represented in the initial state vector: an individual that is captured in the year when it was born always starts in the state Juvenile, while adult females can start in any of the adult states. Between consecutive breeding seasons, individuals can survive or die (represented in the survival matrix). Alive individuals can transition between live states. This transition has two steps: a breeding-probability matrix describes the probability that an individual is pregnant, and a breeding success matrix describes the probability of an individual becoming a successful breeder (i.e. lactating, conditional on pregnancy). Some reproductive state transitions are restricted (Figure 1): juveniles and pre-breeders can transition to become either first-time breeders (SB¹ or FB¹) or pre-breeders (PB). First-time breeders, experienced breeders and skipped breeders can transition to become experienced breeders (SB²⁺ or FB²⁺) or skipped breeders.

The observation process is represented in three event matrices. The first is a matrix of recapture probability, and its parameters represent the recapture probability of live individuals. The second event matrix describes the conditional probability that an individual that was captured in the current season was captured in the early (pregnancy) period of the season. Conditional on the first two event matrices, the third event matrix describes the probability that an individual was captured in the late (post-parturition) period.

Female bats are generally known to exhibit high philopatry to their natal colony (Burland, Barratt, Nichols, & Racey, 2001; Kerth, Safi, & König, 2002), and this is our experience within our study system. Thus, we consider emigration from the area unlikely. Moreover, although our capture season was relatively long (April–September), we consider it unlikely to affect the estimates of between-states transition. Transition to pregnancy happens in the early spring period. Transition between pregnancy and lactation happens when females give birth in late May/June (Linton & Macdonald, 2018).

2.3 | Covariates

We studied how age (zero for juveniles, one for bats in their first summer after birth, etc.), and cohort (the year in which an individual was born, representing early life influences on performance), previous reproduction and weather affect probabilities of survival, pregnancy and lactation. To study age and cohort effect, we used only females of known aged (captured as juveniles). We considered two weather factors, one describing the conditions in winter and the other describing the conditions during the breeding season. The average January–February temperature of the winter preceding the breeding season is likely to influence body condition (depletion of fat reserves) at the end of winter, and thus the ability (or choice) of females to commence pregnancy in spring—bats rely on accumulated fat reserves to survive during hibernation (Jonasson & Willis, 2011). We describe breeding season conditions based on the availability of suitable foraging conditions using an index of foraging time, SFC, based on weather conditions per hour (see Supporting Information, Table S1). As bats are income breeders (Henry et al., 2002), their ability to produce and raise offspring should be strongly influenced by their ability to forage successfully. When studying weather effects on the probability of successful reproduction, we used the April SFC Index of the current breeding season (from 2008 to 2015), while for analyses of survival costs of reproduction we used the April SFC Index of the previous season (from 2007 to 2014).

2.4 | Model selection procedures

To test for age-related patterns of survival and reproduction, and for trade-offs, we imposed different restrictions on the parameters of interest in the transition matrices. We used the Akaike information criterion AICc values (Burnham & Anderson, 2002) as a measure of the support for a model. Datasets used in the analyses, for females of both species separately, can be found in Zenodo repository (Culina, Linton, Pradel, Bouwhuis, & Macdonald, 2018). We fitted all models in the program E-surge (Choquet, Rouan, & Pradel, 2009). We conducted the analyses in three steps.

In the first step, we tested for the presence of age effects on probabilities of survival, pregnancy and lactation. We also tested whether onset of first reproduction and its success varied with age. In this step, we only considered females that were first captured as juveniles (and therefore were of known age and cohort). We fitted several possible models of age dependence of survival, pregnancy and lactation (from full to no age dependence, see Supporting Information results for detailed model definitions). Because the large majority of *M. daubentonii* started to breed in their first year (see Results), we did not test for an influence of age on the probability to become a first-time breeder. We also tested for cohort (year of birth) effects on survival and reproduction throughout life (as an additive effect, i.e. a long-lasting cohort effect), or constrained only to juveniles (i.e. a shorter-term effect of the particular conditions in the year of birth on survival and reproduction of juvenile individuals).

In the second step, we tested whether there were any costs of current breeding to survival and/or future breeding, whether lactation was costlier than pregnancy, and whether there were costs specific to first breeding. In these analyses, we used all females (of known and unknown age), and we kept any cohort or age effect as detected in the previous step, but restricted to known age females only. For the three parameters of interest (survival, pregnancy and lactation), we first sequentially tested whether there was any trade-off with the previous reproductive state. When reproductive state was found to influence a parameter of interest, we additionally tested whether this effect depended on age (again, on the full dataset, but with the age dependence restricted to the females of known age).

In the third step, we tested whether there was support for between-year variation in survival, pregnancy and lactation, and whether such variation depended on our environmental covariates. To test whether there was annual variation in a parameter of interest and whether this variation depended on a female's reproductive state, we added year as an additive covariate or in interaction with the breeding state(s) selected in step 2. Details on model selection with environmental covariates are provided in the Supporting Information.

In all models, we kept the recapture probability dependent on social group. Bats in our populations form social groups that occupy spatially explicit areas. Based on previous work (Culina, Linton, & Macdonald, 2017), we specified 6 social groups in *M. daubentonii* and 7 social groups in *M. nattereri*. All model selection tables are provided in the Supporting Information (Supporting Information Tables S3–S23).

We performed goodness-of-fit (GOF) tests on the unistate capture histories (a common procedure for multi-event models, Pradel, Gimenez, & Lebreton, 2005). Results of the GOF showed a moderate lack of fit in both species (overall $\hat{c} = 4.2$ with $df = 30$ in *M. daubentonii*, $\hat{c} = 3.5$ with $df = 24$ in *M. nattereri*). However, neither the overall test, nor any test component, was statistically significant when the test was conducted on each social group separately.

3 | RESULTS

3.1 | Survival and reproduction in *M. daubentonii* females

Survival of *M. daubentonii* was estimated to be age-dependent, with several models of age-dependent survival gaining similar support (Supporting Information Table S3). All of these models estimated a sharp increase in survival probability between the juvenile and adult stage. However, depending on the model, survival stabilized either straight after this initial increase, or slightly increased up to age 5 and then slightly decreased afterwards (Supporting Information Figure S1). The only supported age effect on reproduction (Supporting Information Table S4) was a slight increase in the probability of pregnancy, and a marked increase in lactation probability for 2-year-old compared to 1-year-old females (Figure 2a). The probability that a pre-breeder starts to breed was extremely low (0.08, 95% CI 0.01–0.41), such that almost all

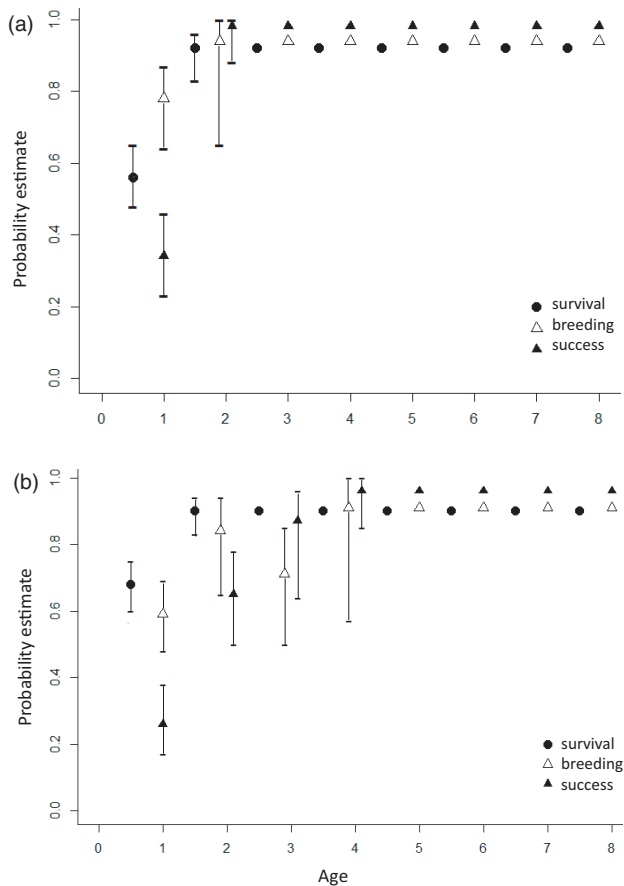


FIGURE 2 Age-related probabilities of survival (black circles), pregnancy (white triangles) and lactation (black triangles) with 95% CI for female (a) *Myotis daubentonii*; (b) *M. nattereri*. Estimates were obtained from the best model in the set of models on age-related survival and reproduction. CI is not given for the estimates that do not change with age. Age 0 is the year in which a bat was born. The survival estimates are plotted so they fall between the two subsequent ages (e.g. between 0 and 1 are survival estimates of juvenile bats) because survival is estimated between the two breeding seasons. Pregnancy and lactation probabilities are plotted on the exact age at which reproduction occurs

females that recruited into the breeding population did so in their first year. Juvenile survival, but not adult survival, pregnancy or lactation varied between cohorts.

Model selection suggested that reproduction is costly to survival (Supporting Information Table S6), but not to reproduction (pregnancy or lactation) in the next season (Supporting Information Tables S7 and S8). Survival of breeders (both successful and unsuccessful) was estimated to be lower than survival of skipped breeders (Figure 3a). Interestingly, experienced successful females (i.e. females that completed lactation) survived at higher rates to the next breeding season compared to failed breeders, while the first-time breeders suffered an additional cost of lactation with 33% reduced survival of successful compared to failed first-time breeders. No other age effect on trade-offs beyond this cost of lactation in the year of first breeding was detected (Supporting Information Table S7), and none of the effects varied between cohorts (Supporting Information Table S8).

Model selection showed that survival, probability of pregnancy and probability of lactation varied between years (Supporting Information Tables S11–S13), but did not support weather factors to explain variation in survival or survival costs of reproduction. The probabilities of pregnancy and lactation did vary between years (Supporting Information Tables S12 and S13), and were largely explained by April SFC Index: 68% of the temporal variation in pregnancy probability and 50% of the variation in lactation probability were explained by SFC, and both parameters increased with available foraging time. Temperature in the previous winter did not explain variation in any breeding parameters.

3.2 | Survival and reproduction in *M. nattereri* females

Model selection supported models with age-dependent survival (Supporting Information Table S14) and reproduction (Supporting Information Tables S15–S18). Survival increased between the juvenile and adult stage and then remained stable. *Myotis nattereri* females showed a more gradual increase in their reproductive parameters compared to *M. daubentonii*—the probabilities of both pregnancy and lactation increased markedly between age 1 and 4 (Figure 2b). The probability of a pre-breeder to become a breeder was estimated to be high (0.70, 0.61–0.78) and age-independent (Supporting Information Table S17). The age of primiparity did not explain variation in the success of the attempt per-se (Supporting Information Table S18), beyond the general relationship between age and breeding success. There was an indication that the probability to lactate might slightly decline after age 4 or 5 (models with or without the decline gained very similar support, Supporting Information Table S16, Figure S2). The probability to be pregnant varied between cohorts (cohort model 16.93 lower AICc compared to a model without the cohort), but this effect was constrained to first-year females.

Model selection did not detect survival costs of reproduction (Supporting Information Table S19): successful breeders survived at the highest rate, followed by unsuccessful breeders, and then by females that skipped breeding (Figure 3b). Breeders (successful and unsuccessful) had a higher probability to be pregnant in the next year compared to females that skipped breeding. First-time breeders were estimated to have similar survival rates to those of experienced breeders, but around 30% lower probability of pregnancy in the next year. Model selection provided similar support for models with and without a difference in future probability of pregnancy for successful and failed first-time breeders; if costly, future pregnancy probability was estimated to be reduced by 40% after lactation. Two models of the effect of current breeding on future lactation probability gained similar support: in one, future success did not vary with the current success, while in the other failed breeders experienced around 13% higher breeding success in the future.

Model selection on annual variation in survival and breeding parameters supported such variation in survival, as well as an influence of the April SFC Index on pregnancy probability (explaining 79% of time-variation in breeding success) and lactation probability of first-time breeders. Winter temperatures were not selected as explaining

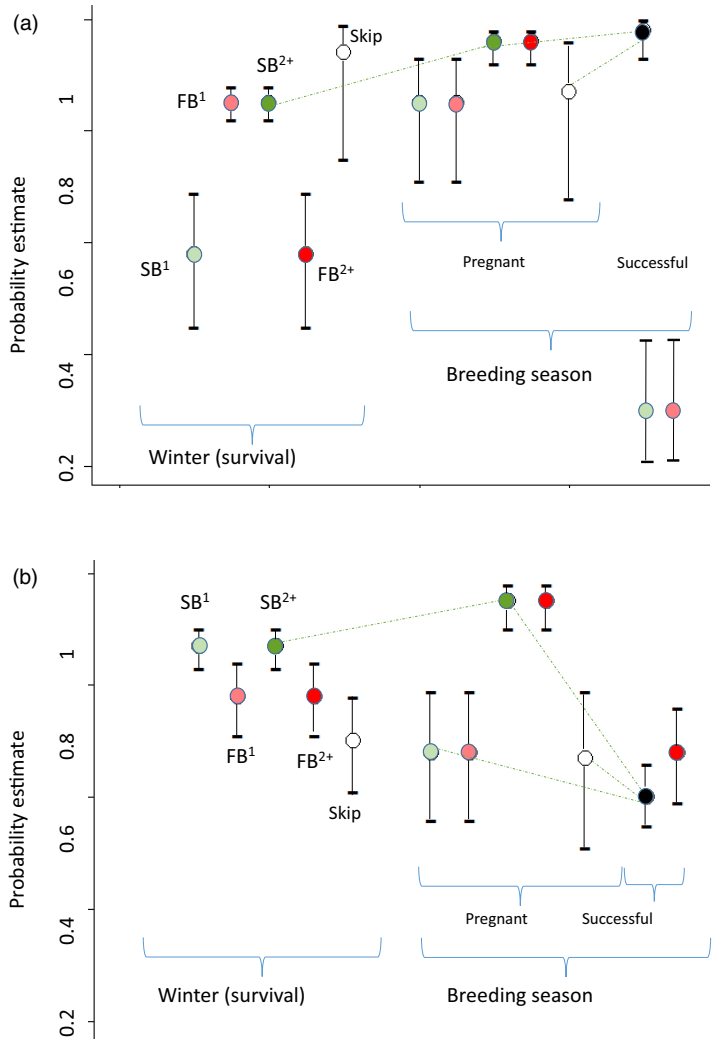


FIGURE 3 Estimates and 95% CI of probabilities of survival between $t-1$ and t breeding season, and pregnancy and lactation in the breeding season t for *Myotis daubentonii* (a) and *M. nattereri* (b) females of different states in season $t-1$: successful/failed first-time breeders (SB¹: light green, FB¹: pink), successful/failed experienced breeders (SB²⁺: green, FB²⁺: red), or skipped breeders (empty circles). The overall estimated future success (probability of survival, pregnancy and lactation) is provided as the last set of circles. In *M. daubentonii*, all experienced females had the same lactation probability (black circle). In *M. nattereri*, all but FB²⁺ females had the same lactation probability

variation in survival or reproduction, and there was no indication that any of the states experienced different selection pressures over time.

4 | DISCUSSION

Our study revealed the existence of several, to our knowledge previously unknown, trends in survival and breeding of small, long-lived income breeders with fast metabolic rates, and detected remarkable differences in the recruitment tactics and survival-reproduction trade-offs of two closely related, sympatric species. The results we obtained, using a robust novel statistical framework that describes the life cycle of females, indicate that bats (as long-lived income breeders) show some of the patterns expected for long-lived capital breeders, and some for short-lived income breeders.

4.1 | Age and costs of first reproduction

Delayed breeding is expected to be an optimal tactic of long-lived species with costly early reproduction (Mourocq et al., 2016). First reproduction might be costly to survival because younger

animals have not fully completed growth (and thus need energy to grow; Metcalfe & Monaghan, 2001), and/or they need to allocate more energy to reproduction due to being inexperienced. In our study, two long-lived species were shown to exhibit remarkable differences in age and cost of first reproduction. *Myotis daubentonii* juveniles had a high probability to become breeders in the following year (c. 80%), despite the very low success of this first attempt (c. 30%), and high survival costs of lactation for first-time breeders (c. 33% lower survival probability). On the other hand, the probability of pregnancy of first-year *M. nattereri* females was much lower (c. 57%), while inexperienced adults (pre-breeders) had a relatively high chance to become breeders (70%), with no observable costs of this first breeding. This pattern fits well with our finding that the probability of successful pregnancy increases with age in *M. nattereri*, but not in *M. daubentonii*, suggesting that it might be more beneficial to delay first breeding if older females have increased chances of weaning their offspring due to breeding-experience-independent age effects.

Drastic reduction in survival due to lactation in first-time *M. daubentonii* breeders is probably a result of the reduced time that an inexperienced, young female has to build up fat reserves

before winter after spending a considerable amount of energy on lactation (Moyes et al., 2011). This possibility could be tested using detailed data on the weight of young and adult females at the end of failed pregnancy, lactation, and just before hibernation. The costs of first reproduction at a young age can also explain our inability to detect the costs of first reproduction to *M. nattereri* females—delayed primiparity in this species (as shown in our study) is likely the reason why first-time and experienced breeders have an equal probability of successful pregnancy and survival. The lack of detection of any age effects on the success of the first breeding attempt in *M. nattereri* females might also be a result of only high-quality individuals, or individuals in good condition, starting to breed at a young age (Lemaître et al., 2015). Why there would be such quality differences in *M. nattereri* but not in *M. daubentonii* is, however, unclear, and the question of why these two species show different life-history tactics, and why *M. daubentonii* females attempt breeding in their first year despite the costs, thus remains unanswered.

4.2 | Trade-offs—differences between species

Life-history theory predicts that costs of reproduction in long-lived species with low mortality rates will be reflected in future reproduction rather than survival, while the opposite is expected for short-lived breeders (Hamel et al., 2010). Based on our results, it seems that in bats both of these theories hold: in *M. daubentonii* reproduction affected future survival (but not future reproduction), while in *M. nattereri* there was indication of low costs of lactation to future reproduction (successful females have lower success rates at their next pregnancy), but no survival costs of reproduction. Observed lack of costs to future breeding (apart from a low cost of lactation in *M. nattereri*) is in line with the breeding mode of bats—as income breeders, success of pregnancy should depend on female condition (Rughetti & Toffoli, 2014), and condition likely depends on the quality of the current breeding season (as we also found in this study) rather than on the female's physical state in the previous breeding season. Furthermore, reproduction in *M. nattereri* did not reduce over-winter survival, likely because these bats also feed during hibernation period (Hope & Jones, 2012) meaning that they can compensate for any lack of fat reserves incurred during reproduction.

Our results also indicated that experienced *M. nattereri* females embark on lactation only if they are in good physical condition (as also found in a capital breeder, the Alpine ibex, Rughetti et al., 2015)—females that lactated survived almost 30% better than failed females.

4.3 | Actuarial and reproductive senescence

We found indication for some senescence in survival to occur after the age of 4 or 5 in *M. daubentonii* females, but we did not detect senescence in reproductive parameters. Such decoupling of senescence patterns between traits has been observed more often

and shown to be especially likely in long-lived species of birds and mammals (Bouwhuis et al., 2012). No senescence was detected in *M. nattereri*. Given the longevity of our species, even the 8 years of our dataset might not have been long enough to detect senescence (Nussey et al., 2006; Warner, Miller, Bronikowski, & Janzen, 2016). Two much longer studies (Greiner et al., 2014 for 18 years, and Fleicher et al. 2017 for 19 years) also detected no decline in reproductive performance or survival in female *Saccopteryx bilineata* and *Myotis bechsteinii* bats, respectively. Davis (1966) did find that survival of *Pipistrellus subflavus* decreased after the survival peak at 3.5 years of age, but this study used a cross-sectional analysis, which may not accurately reflect within-individual changes with age when there is selective disappearance of individuals with specific phenotypes (Nussey, Coulson, Festa-Bianchet, & Gaillard, 2008). Finally, we used only females in our study, while in polygamous mammals, such as bats, declines in reproductive performance with age may be expected to be more pronounced in males (Greiner et al., 2014), the sex that experiences stronger within-sex competition for mates (e.g. Carranza & Pérez-Barbería, 2007).

4.4 | Environmental effects

We found evidence that weather conditions influence breeding parameters (breeding probability and success), and that this effect is similar in two different bat species. The dependence of breeding parameters on environmental conditions has previously been shown both in capital breeders (e.g. Hamel et al., 2009, 2010) and income breeders, including our two study species (Linton & Macdonald, 2018). Bat populations are likely to be sensitive to weather conditions experienced during the breeding season (Jones et al. 2009) because females rely on constant intake of food during pregnancy (income breeders, Henry et al., 2002).

We did not find any evidence that survival costs of reproduction depend on the weather conditions, nor that any particular group of breeders (successful, failed, non-breeders, first-time breeders or older breeders) experience different between-year variation in survival or breeding parameters. Although some studies have shown that, in large mammals, costs of reproduction are higher under unfavourable conditions (e.g., Garnier et al. 2016; Tavecchia et al., 2005, but see Moyes et al., 2011), there is no such evidence for income breeders (Descamps, Boutin, McAdam, Berteaux, & Gaillard, 2009).

4.5 | No long-lasting cohort effects

We did not detect any long-lasting effects (i.e. after the first year) of the cohort (year of birth) on survival, reproduction or trade-offs in either of our study species. Although silver spoon effects, where the conditions experienced in the first year of life have long-lasting effects on adults, have been demonstrated in some large mammals and birds (e.g. Burness et al. 2000; Cam & Aubry 2011), they seem to be less common in small mammals that are income breeders (Descamps et al., 2008) or species that use a brood reduction tactics, which may relate to variation in the relative strength of selection in early and

late life and warrants further investigation (Vedder & Bouwhuis, 2018).

5 | CONCLUSIONS

Our study is, to our knowledge, the first to address survival–reproduction trade-offs in long-lived income breeders. Our results, obtained using a robust and novel statistical framework, indicate that species with this type of life history exhibit a mixture of patterns between long-lived capital breeders and short-lived income breeders. Currently, there is a lack of studies on bats in evolutionary ecology, although the group displays a unique combination of traits (including the ability to fly). We therefore call for more studies to be conducted in similar study systems, increasing our ability to fully understand the evolutionary origin and fitness significance of trade-offs and senescence.

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AUTHORS' CONTRIBUTIONS

This study is part of a larger programme conceived by A.C., D.M.L. and D.W.M., based on field data collected by D.M.L. and funded by a grant to D.W.M. Within that programme, this paper was conceived by A.C. in discussion with D.M.L. and D.W.M., and A.C. constructed the base of the modelling framework, conducted the analyses, and wrote the manuscript; D.M.L. collected the data, helped to interpret the data, contributed knowledge on bat biology, and revised the manuscript; R.P. substantially contributed to the analysis (model construction) and helped to revise the manuscript; S.B. provided substantial input on the manuscript and its revision; and D.W.M. contributed to manuscript revision.

DATA ACCESSIBILITY

Data used in the analyses (capture histories of female bats) are deposited in Zenodo repository under CC-BY licence, <https://doi.org/10.5281/zenodo.2222410> (Culina et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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