Running Head: Lay date variation in tree swallows

Full lifetime perspectives on the costs and benefits of lay date variation in tree swallows

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This is the author manuscript accepted for publication and has 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: 10.1002/ECY.3109

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ABSTRACT

Animals must balance various costs and benefits when deciding when to breed. The costs and benefits of breeding at different times have received much attention, but most studies have been limited to investigating short-term season-to-season fitness effects. However, breeding early, versus late, in a season may influence lifetime fitness over many years, trading off in complex ways across the breeder's lifepan. In this study, we examined the complete life histories of 867 female tree swallows (*Tachycineta bicolor*) breeding in Ithaca, New York, between 2002 and 2016. Earlier breeders outperformed later breeders in short-term measures of reproductive output and offspring quality. Though there were weak indications that females paid long-term future survival costs for breeding early, lifetime fledgling output was markedly higher overall in early-breeding birds. Importantly, older females breeding later in the season did not experience compensating life-history advantages that suggested an alternative equal-fitness breeding strategy. Rather, most or all of the swallows appear to be breeding as early as they can, and differences in lay dates appear to be determined primarily by differences in individual quality or condition. Lay date had a significant repeatability across breeding attempts by the same female, and the first lay date of females fledged in our population was strongly influenced by the first lay date of their mothers, indicating the potential for ongoing selection on lay date. By examining performance over the entire lifespan of a large number of individuals, we were able to clarify the relationship between timing of breeding and fitness and gain new insight into the sources of variability in this important life history trait.

Keywords: lay date, life history, alternative strategies, lifetime fitness, *Tachycineta bicolor*, timing of breeding, tree swallow

INTRODUCTION

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Timing of breeding is one of the most important determinants of organismal fitness. Across a broad variety of taxa, the decision of when to breed determines what food resources will be abundant during each stage of reproduction (e.g. mink, Ben-David 1997; sea ducks, Love et al. 2010), the types and variety of nest sites available for breeding (e.g. house martins, Piersma 2013), the prevalence of parasites and predators that may harm the adult or its offspring (e.g. squirrels and hares, O'Donoghue and Boutin 1995; cliff swallows, Brown and Brown 1999), and the energy budget available for investment into other life history traits (e.g. wheatears, Low et al. 2015). Previous researchers have documented the many costs associated with breeding at suboptimal times (blue tits, Nilsson 1994; sandpipers, McKinnon et al. 2012; owls, Toyama et al. 2015), and the importance of proper timing has become especially clear in circumstances in which environmental conditions have recently deviated from historical norms (e.g. flycatchers, Both and Visser 2001; grouse, Ludwig et al. 2006; deer, Plard et al. 2014). Indeed, changes in reproductive phenology are one of the most pervasive responses observed to global climate change (squirrels, Reale et al. 2003; wide variety of taxa, Visser and Both 2005; frogs, Benard 2015, red deer, Moyes et al. 2011; wide variety of plants, Cleland et al. 2012).

In seasonally breeding birds, individuals that lay their eggs earlier in the season generally fledge more young than do individuals that lay later (e.g. Hochachka 1990, Goodenough et al. 2009, Öberg et al. 2014). This could be because early breeding offers greater access to food quantity (e.g. Schoech et al. 2004, Ardia et al. 2006) or quality (Twining et al. 2018), availabilty of better nesting sites (e.g. Rosvall 2008), access to better mates (Kirkpatrick et al. 1990) or more time to assess them (Ferretti and Winkler 2009), additional time for undertaking a greater number of reproductive attempts (e.g. Monroe et al. 2008, Morrison et al. 2019), or the chance to breed before high background rates of mortality take one or both of the parents (Goutis and Winkler 1992).

Much past research has attempted to parse two effects that might explain why early breeders are more successful (reviewed in Verhulst and Nilsson 2008). A quality effect would appear as a decline in reproductive output over the course of a breeding season because individuals of higher quality or condition are breeding before birds of lower quality or condition. (For some of the complexities in different concepts of individual quality see Bergeron et al. 2011). In contrast, a date effect could lead to a seasonal deterioration in environmental

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conditions such that all individuals have lower success later in the season. These two effects have traditionally been treated as alternatives, and several studies have attempted to tease them apart by experimentally manipulating timing of breeding (Wardrop and Ydenberg 2003, Dawson 2008, reviewed in Verhulst and Nilsson 2008, Harriman et al. 2017). However, for the quality effect to be supported, there must be a reason why high-quality birds should choose to breed earlier, and, to the extent that advantages of earlier breeding are environmentally derived, as the date effect suggests, rather than representing true alternatives, these two effects are not really distinct and may best be seen as causally linked (cf. Verhulst and Nilsson 2008).

There is another persistent question about lay dates: if, as long thought (Perrins 1970), breeding birds are attempting to match their reproductive efforts with an optimal time to breed, why do some members of the population breed later than would be ideal? The most likely explanation is that breeding early is difficult – that it imposes challenges that only some individuals are able to overcome. Such challenges could include enduring harsh early-season environmental conditions such as inclement weather (e.g. Ramos et al. 2002), low food availability (e.g. Young 1994, Bowlin and Winkler 2004), high levels of predation (e.g. Borgmann et al. 2013), or competition for scarce nesting sites or mates (e.g. Smith 2006). Several studies of timing of breeding have explored the connection between quality and date experimentally (reviewed in Verhulst and Nilsson 2008) or by examining facets of fitness beyond reproduction (Brinkof et al. 2002, Brown et al. 2015, Low et al. 2015, Needham et al. 2017, Evans et al. 2019). However, in the latter cases, breeding adults have usually been followed only to the season just after the focal breeding attempt. All of these environmental costs of breeding early provide a mechanistic link between quality and date and reinforce the non-independence of these effects.

When multi-trait data are available over the entire lifespans of many individuals, rather than try to tease apart two effects that are so tightly linked, we decided instead to recast the research to distinguish between two more fundamental hypotheses about the origins of life history variation: Is reproductive output highest early in the season because early breeders are of higher quality and do better across the board, or are early breeders paying a price in the form of lower performance elsewhere in their lives? These hypotheses pertain to one of the longest-running questions in evolutionary and behavioral ecology (Maynard Smith 1982, Werner and

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Sherry 1978, Stamps et al. 2013): are variations in the behavior and reproduction of individuals within populations the result of different individuals pursuing different strategies or the result of all or most individuals all essentially pursuing the same strategy with individual variations the result of the vagaries of chance and circumstance? If there is a life-history trade-off between allocations to parental effort vs. self-maintenance (e.g. Stearns 1976, Winkler and Wilkinson 1987), birds that seem to underperform in one aspect or stage of their lives may compensate elsewhere in their life history. We would best be able to detect such a trade-off with full life-cycle data: the full consequences of a lay date decision may only become apparent over long timescales.

Hypotheses and predictions: Here we take a full lifespan approach to testing these two hypotheses, analyzing fifteen years of life history data from a population of tree swallows (*Tachycineta bicolor*) in upstate New York. A negative correlation between lay date and single-season reproductive output is well-documented in this population (Winkler and Allen 1996), but the full-lifetime perspective on lay date variation has not been explored. We tested the two fundamental hypotheses mentioned above:

Hypothesis 1: Variation in lay dates of tree swallows is the result of variation in individual quality. Under this hypothesis, which can include both quality and date effects, we assume that lay date is constrained by the high costs of breeding early, costs that only high-quality females are able to bear. If only those females in the best condition are able to surmount the obstacles that prevent an early reproductive effort, then this could explain why only some females can reap the benefits of early breeding. Under this integrated „Quality Hypothesis“, lower quality females would be constrained to breed later in the season when resources are more abundant. Because this hypothesis posits a difference in individual quality between early and late breeders, it predicts that early breeders should be superior to late breeders across all components of fitness. Early breeders should fledge relatively more offspring in better condition over the course of their longer lives. In contrast, later breeders should fledge relatively fewer offspring in poorer condition over the course of their shorter lives.

Hypothesis 2: Variation in lay dates of tree swallows is the result of different individuals pursuing alternative, equal-fitness, life history strategies. Under this hypothesis, early and late breeders do not necessarily differ from one another in overall quality or fitness. Instead, they

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make a different trade-off between lay date and other life history components. For example, early breeders may excel in gathering food at times of year when resources are scarce and subject to greater uncertainty, but this may come at the cost of greater energetic expenditure and lower body condition, both of which could contribute to reduced parental survival. In contrast, late breeders may avoid some of the self-maintenance costs of breeding in colder spring temperatures, but pass these costs on to their offspring, who would fledge later in the summer when reduced time to migration may be disadvantageous. This Alternative Strategies Hypothesis predicts that early and late breeders use different strategies to manage the costs and benefits of breeding early such that their life histories will differ markedly in kind, but not in overall fitness (cf. Tarwater and Beissinger 2013). Our sample of breeding years encompassed considerable diversity in breeding conditions, and the Alternative Strategies Hypothesis predicts that earlier and later breeders will each excel in different life history components, with earlier breeders overall exceeding later breeders in some components of fitness and later breeders overall out-performing earlier breeders in others.

The contrasting predictions of the two hypotheses are summarized for each fitness metric being tested here in Table 1.

Complexities in assessing lay date variation: One of the chief difficulties in evaluating the relationship between lay date and its fitness consequences in long-term data is that lay date is not necessarily stable across a female's lifetime. A female that breeds relatively late in one year may breed relatively early the following year, and vice versa. Understanding the costs and constraints that accompany variation in lay date therefore requires that we understand the relevant timescales over which the effects of lay date are felt. Fitness costs incurred as a result of breeding at a suboptimal time may be relatively short-lived, affecting each breeding attempt independently of all others, or they may accumulate across an individual's lifetime, with each set of costs adding up to greater and greater consequence. It is also possible that some reproductive events exert a greater impact on an individual's fitness trajectory than do others. This may be especially likely for an individual's first reproductive attempt. Because young females breeding for the first time must grapple with all of the typical costs of reproduction as well as their own inexperience, it is possible that costs incurred then may influence a female's life history for the rest of her life. In this study, we evaluate each of these possibilities by considering the fitness

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consequences of each female's current lay date, her previous lay date, and the lay date of her first reproductive attempt.

It has also long been appreciated (von Haartman 1982) that lay dates can affect avian reproduction both through "absolute" and "relative" timing. If external effects from the environment are most important, then absolute calendar date is going to be most informative. On the other hand, if interactions between members of the breeding population dictate optimal timing of reproduction, when a female lays relative to the others in her local population may better account for lay date effects on fitness.

Finally, any life-history view of lay date variation must be prepared to address potential selective effects on trait variation, and our long-term data provided us the opportunty to assess mother-daughter similarities and the potential for heritable variation in this key life-history trait.

METHODS

Study Species. Tree swallows are migratory aerial insectivores that breed across much of North America. Tree swallows are one of the earliest migrants to return to their breeding grounds, and they must contend with adverse weather up to six weeks before and during early reproductive attempts, sometimes with disastrous consequences (Hess et al. 2008). They are also one of the last to migrate to wintering latitudes in the fall, a characteristic that is likely facilitated by their ability to subsist on *Myrica* sp. berries at times of year when flying insects become unavailable (Winkler et al. 2011, Piland and Winkler 2015). Tree swallows are secondary cavity nesters, and intense competition for scarce nesting sites has probably shaped much of their biology. As in other species, a negative correlation between lay date and clutch size is well documented (Winkler and Allen 1996), with at least some of the variation in lay date correlated to variation in female flight performance (Bowlin and Winkler 2004). Earlier laying birds also exhibit higher immunocompetence when exposed to novel antigens (Hasselquist et al. 2001, Ardia 2005).

Study Sites. This study relied on data collected from a population of tree swallows breeding near Ithaca, in Tompkins County, New York (42°28' N, 76° 29' E). The study population was first established in 1985 at the Cornell University Experimental Ponds Unit 1. Since that time, additional nest boxes have been variably added and removed at nine other study sites distributed throughout Tompkins County. For the present study, we used data collected from females

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breeding at five sites that were well-established and regularly monitored with consistent protocols from 2002 onward. At each site, between 22 and 260 nest boxes of the same design (for further details see Winkler and Allen 1996) were placed ~20 m apart on free-standing metal poles or affixed to existing wooden fence posts in open habitat suitable for tree swallow breeding.

Beginning in April of each year, nest boxes were checked every 2-3 days for nesting material that might indicate the presence of nest-building swallows. As breeding progressed, observers noted the presence and number of any eggs or nestlings. Female parents were captured in the box by hand or using a nest trap during incubation to be banded with a USGS aluminum band and measured (head + bill length, wing length, and mass). Many male parents were captured and processed in the same way during the nestling period, but male capture rates were sufficiently low that our analyses of adult reproductive costs and benefits are here limited to females only. A small (<100 μL) blood sample was also taken by brachial venipuncture at this time. Nestling swallows were similarly banded, measured, and blood-sampled between days 6 and 12 after hatching. During the course of this study, a number of additional observational studies and experiments were ongoing. Therefore, in particular years at particular sites, a subset of birds was subjected to treatments or sampling regimens that fell outside the scope of the long-term monitoring effort. Depending on the severity of the treatment and its anticipated effects on tree swallow fitness, we excluded some of these nesting attempts from our final dataset (see 'Data Filtering', next).

Data Filtering. In this study, we sought to track the fitness of individual females across their entire adult lives. To accomplish this goal, we needed to know the age of each swallow in our population. Female tree swallows included in our dataset could be aged in one of two ways: first, swallows fledged from one of our study sites could be aged based on the year in which they were first banded as nestlings; second, swallows who first appeared at our sites as unbanded adults could be aged based on plumage. This was possible because female tree swallows exhibit delayed plumage maturation, with one-year-old females (henceforth "yearlings") having predominantly brown upperparts and females two years old and older (henceforth "older females") wearing male-like iridescent blue-green plumage (Cohen 1980, Hussell 1983). Thus, females who were first banded in brown plumage could be reliably aged as being yearlings, still

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238 in their first complete year of life. Approximately 40% of the breeding females in our study
239 population are first captured and banded in non-brown plumage (i.e., older females), and these
240 were excluded from our dataset owing to our inability to reliably estimate their age and entire life
241 history.

242 The second requirement for inclusion in our dataset was that female swallows of known
243 age must have bred in one of our boxes as yearlings. Of the 494 cases in which a female fledged
244 from our study population and returned to breed there, 388 (78.5%) bred as yearlings. The
245 remaining 106 (21.5%) returning females that first bred in our study area as older females were
246 excluded from our final dataset, as we could not know whether they had been non-breeding
247 floaters (Stutchbury and Robertson 1987) or bred undetected in unmonitored areas during their
248 first year of life. In either case, our lack of information concerning their activities would have
249 made spurious any effort at linking their lay date and fitness.

250 Having assembled this dataset of all reproductive attempts for every female tree swallow
251 at our sites known to have bred as a yearling, we then evaluated individual reproductive attempts
252 for inclusion or exclusion from our final analysis. We required that every female's yearling
253 breeding attempt had complete information regarding its lay date and fate and that the nest had
254 not been subjected to severe manipulation. If any of these criteria were not met, we excluded the
255 female from further analysis. We likewise required that all older female attempts had complete
256 information regarding lay date and fate, but for older female attempts that were manipulated in
257 the course of a secondary observational study or experiment, we evaluated the severity of
258 sampling or treatment to determine the best course of action to take. Treatments that involved
259 non-destructive sampling of adults or nestlings (e.g. collection of a primary feather, additional
260 blood samples, or immune assays) were allowed to remain in our final dataset (see Orzechowski
261 et al. 2019 for negligible life history effects of bleeding), as were nests subjected to short-term
262 treatments designed to measure a behavioral or physiological response over a restricted period of
263 time (e.g. less than a few hours). Nests subjected to destructive sampling or longer-term
264 manipulations (e.g. manipulation of nest materials, microbial environment, stress physiology,
265 energetic expenditure, egg or brood number, or predator exposure) were treated in one of two
266 ways. For analyses involving single-season reproductive output, such nests were excluded from
267 the point in the nesting cycle at which the treatment was expected to have had an effect. For

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example, an experiment that involved transplanting nestlings between nests would have been included in analyses of clutch size but excluded from analyses of number fledged. For analyses involving lifetime reproductive output, we adjusted the female's lifetime number fledged to reflect the expected number of offspring she would have produced in the absence of the experimental treatment. To arrive at this adjustment, we calculated for each female the mean deviance in number fledged from the population means for her age class (yearling vs. older female) in each of her unmanipulated years of breeding, and then applied this deviance to the population mean for her age class in the year(s) during which she was manipulated. For example, a female whose unmanipulated reproductive attempts resulted in an average fledge number that was two nestlings higher than the average fledge number of other members of her age class in each relevant breeding year would have been assigned a fledge number that was two nestlings above the population mean in each year for which her reproductive success was unavailable. We chose to perform this adjustment because longer-lived females were necessarily more likely to have been subjected to one of these experimental treatments simply because they presented more opportunities for manipulation. Thus, this adjustment enabled us to eliminate a severe bias in representation of shorter-lived vs longer-lived females. For those particularly concerned about any of these sorts of adjustments, we also ran the analyses for lifetime performance leaving out any female that had had a disqualifying manipulation in any of its seasons. The reduced and biased sample lent these analyses less statistical power, and one of the analyses produced the same result as the corrected version (Appendix S1: Table S13 vs. S14), while the other returned the null model as the most highly supported (Appendix S1: Table S11 vs. S12).

Statistical Analyses.

Life history and fitness metrics. To evaluate whether early and late breeders vary in lay date due to differences in overall quality or due to differences in life history strategy, we examined the relationship between lay date and a variety of short- and long-term fitness outcomes using a combination of general and generalized linear mixed effects models (*lme4* package in R v.3.5.1; Bates et al. 2015, R Core Team 2018). Fitness benefits and costs for breeding females were analyzed in three aspects: reproductive output, offspring quality and parental survival. Within reproductive output, we analyzed three components that, combined, led to number fledged: *clutch size* (the number of eggs in the first clutch laid by a female each season); whether or not any young were produced (0 or 1; henceforth "*fledging success*"); and if

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successful, *number fledged*. (To recall the distinct definitions used for fitness components, we henceforth standardize and italicize their names—see Table 1.) Making the distinction between *fledging success* and *number fledged* allowed us to remain clear about reproductive outcomes that may have fundamentally different causes and consequences. The former was analyzed as a binomial response whereas the latter (because all the zeros in the distributions of number fledged are removed by only considering successful females) was analyzed as a Gaussian response.

To assess offspring quality, we measured *nestling mass* prior to fledging and *fledgling recruitment* to the breeding population. Tree swallows are highly dispersive, with only about 4% of fledged offspring returning to breed at the sites from which they fledged (Winkler et al. 2005). Thus, *fledgling recruitment* cannot be taken as a precise measure of the percentage of young surviving to breeding age. Rather, we analyze it here primarily to see if there is any suggestion that the timing of reproduction may influence the quality of offspring and their probabilities of recruitment.

To assess the effect of lay date on parental survival, we relied on female returns to the breeding site in the following year. Tree swallows do not necessarily breed at the same site every year that they survive, and the recapture histories of individuals occasionally include gaps in which a succession of years of regular recaptures is broken by a year in which the bird was not captured, followed by a year or years in which the same individual is captured again. For all analyses of adult *return rate* reported here, we used a corrected return rate which counts the bird as having been alive in any of the gap years which were bracketed by years before and after recapture. The dispersal of breeding adults from one site to another in a subsequent year could be a problem for interpretations of adult female survival rates; however, only about 14% of females (and of these, mostly younger females) breeding in this population disperse to a new breeding site (Winkler et al. 2004) after breeding in our study areas. Also, because female tree swallows are straightforward to capture in the nest with built-in traps once the clutch is complete, our recapture rate for surviving females is very high. We thus base the analyses of female breeder survival here on direct recapture rates, but we also provide in Appendix S1 an analysis conducted with Program MARK (White and Burnham 1999) that produces the same qualitative results.

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In addition to the single-season fitness metrics outlined above, we examined *lifetime fledging success* and *lifetime number fledged* of successful females as holistic, integrated measures of reproductive output and survival over each individual's entire life (Table 1).

Testing hypotheses: Under the Quality Hypothesis being tested, females differ in lay date due principally to variation in overall quality, and we would expect that earlier breeding would correlate with better outcomes across all life history metrics. Under the Alternative Strategies Hypothesis, on the other hand, we would expect early lay dates to be associated with increased reproductive output, but reductions in offspring quality or adult survival (Table 1).

Each life history metric was coded as a response variable, while lay dates from various seasons in the females' reproductive lifetimes were included as fixed effects in separate models. In addition to lay date, we included a number of other fixed and random effects that varied by model type (Table 1), and that were held contant across multiple models for the same response variable. When lay dates were excluded from a particular model, these other variables in combination thus represented a null model that incorporated sources of variation outside of lay date that we believed *a priori* to be important in influencing the response variable under examination. Because clutch size is very strongly related to lay date in tree swallows (Winkler and Allen 1996, Winkler et al. 2002) and other *Tachycineta* swallows (Winkler et al. 2014), we included *clutch size* as a fixed effect in analyses of reproductive output to gauge the direct and indirect effects of lay date on reproduction. Chick age at measurement was included as a fixed effect in models of *nestling mass* to account for the expected larger size of nestlings measured later in the nesting cycle (Winkler and Adler 1996, Winkler et al. 2011), while *number fledged* was included as a fixed effect to account for variation attributable to increased sibling competition in larger broods. For models of adult *return rate*, single-season *fledging success* was included as a fixed effect, since reproductive failure may influence the probability of future dispersal and apparent death (Winkler et al. 2004), and female age was included as a fixed effect (in models involving older females, see below) to account for the possibility that females may be less likely to survive to the following year as they age, irrespective of their lay dates. In models of *fledgling recruitment* (in which individual fledglings were the focal unit of analysis), we included maternal age class as a fixed effect, since offspring quality could differ between yearling and older breeders. We did not code age class as a fixed effect in any other analyses

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because we analyzed yearling and older female attempts separately (see below). Current year was coded as a random intercept in all single-season models to account for annual variation in environmental conditions, and breeding site was coded as a random intercept to account for spatial variation in breeding conditions. In lifetime models and in single-season models that included multiple attempts by the same female, we included hatch year as a random intercept to account for cohort-level variation. We also included female identity as a random intercept in any models that included multiple attempts by the same female to account for the non-independence of such reproductive efforts. For models of *fledgling recruitment*, our random error structure included intercepts for nest identity, natal site, and natal year. For models that examined *clutch size*, *number fledged*, and *nestling mass,* we used a Gaussian distribution with one exception: the very long right tail of the distribution of *lifetime number fledged* precluded treating it as a Gaussian variate, and a Poisson distribution was used instead. For models of *fledging success*, adult *return rate* and *fledgling recruitment* we used a binomial distribution.

For each fitness metric under study, we used an information theoretic approach (Burnham and Anderson 2004) and Akaike's information criterion (AIC) to rank models according to their relative fit to our data, corrected for the number of parameters. There has been a great deal of development of methods for model selection in ecology in recent years, especially in Bayesian methods (reviewed in Hooten and Hobbs 2015), and some of the more sophisticated methods for hierarchical model structures (e.g., WAIC) might be tempting to apply here (cf. Gelman et al. 2013). We ran each set of candidate models with hierarchical random effects (e.g. site nested within year), but, after considering the degree of replication we could achieve in the random effect structures and the fact that we had no research rationale for interpreting the random effects, we limited ourselves here to simple non-hierarchical random effects. None of these hierarchical models yielded results for the fixed effects qualitatively different than those presented here.

We compared each set of candidate models against a null model that excluded lay date. We considered any models that outperformed this null model by at least 2 to be well supported. Within the resulting group of supported models, we gave preference to models with fewer parameters and which were more than ΔAIC of 2 from the rest. We fitted each candidate model using maximum likelihood. For fitness metrics that relied on a Gaussian distribution, we refitted

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our best-supported models using restricted maximum likelihood (REML), which provides more precise parameter estimation. Similar REML-based methods are not well-established for models that utilize a binomial or Poisson distribution. All parameter estimates that we report for best-supported Gaussian models are taken from those refitted using REML. All parameter estimates that we report for best-supported binomial and Poisson models are based on estimates derived from maximum likelihood. In the interests of space, we report in the results only the P-value and conditional R^2 of mixed model fits. Marginal R^2 values (which assess only the explained variance of the fixed effects) and coefficient values and their standard errors are reported in the tables in Appendix S1.

The relevant time scale of lay date effects. For all analyses of lay date, each season's lay date for a given female was taken to be the date that she started her first clutch in that season. In full life-cycle data, there are lay dates from at least three important seasons to be considered (Table 2). To estimate short-term effects of lay date variation on fitness, we used lay date in the current season. To estimate the longer-term effects of lay date variation on fitness, we used lay date from the previous season. Finally, we used lay date from the female's yearling season to account for fitness consequences of lay date variation arising from each female's first reproductive experience. For each of the season's lay dates that we tested, we tested both absolute (1 = 1 May) and relative (1 = day of the earliest clutch in our dataset each year) lay dates. Finally, we tested each lay date variant as both a linear and a quadratic predictor of fitness to account for the possibility that females laying too early, as well as too late, might suffer greater costs.

Because yearling and previous lay dates could only be examined for females breeding for at least the second time, we subsetted our data to ensure that different lay dates from the different seasons were being compared using the same dataset. For models investigating single-season fitness metrics, we compared the effects of yearling, current, and previous lay dates on reproductive output, *nestling mass*, and *return rate* among those females breeding for at least the second time (i.e. all older female attempts). A second analysis compared the effects of current lay date on reproductive output, *nestling mass*, and *return rate* among females breeding for the first time (i.e. all yearling attempts).

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For models of *offspring recruitment*, which were carried out from the perspective of individual nestlings, we ran a single analysis that examined the effect of current lay date (i.e. of the nest from which the nestling fledged) on the probability that the fledgling would return to our study area as an adult. For models of lifetime fitness, we compared the effects on long-term fitness outcomes of both each female's yearling lay date and her average lay date over all reproductive attempts she undertook.

Mother-daughter comparisons of lay dates and repeatabilities. Within our existing dataset of 867 female swallows, we identified 113 instances in which a female's daughter had recruited into our study population and bred in her first year of life, and of these, a further 32 instances in which both mother and daughter survived and bred as two-year olds. This pairing of mothers and daughters enabled us to examine the relative influence of maternal lay date, natal environment, and contemporary environment in determining each daughter's timing of breeding. We constructed a linear mixed effects model in which each daughter's absolute yearling lay date was coded as the response variable, and her mother's absolute yearling lay date, average maximum temperature (a determinant of food availability; Winkler et al. 2013) during her natal period, and average maximum temperature immediately prior to her yearling breeding attempt were coded as fixed effects (Table 3). Maternal identity was included as a random intercept to account for the potential non-independence of data arising from sisters raised by the same mother, while breeding year and site were included as random intercepts to account for temporal and spatial variation not captured by our temperature metrics. For two-year-old females, we constructed a similar linear mixed effects model in which each daughter's absolute two-year lay date was coded as the response variable, and her mother's two-year lay date, daily maximum temperatures during her natal period, and daily maximum temperatures immediately prior to her second breeding attempt were coded as fixed effects. Again, we coded maternal identity, breeding year, and site as random intercepts. Temperature data used in these analyses were collected from a nearby weather station monitored by the Northeast Regional Climate Center (http://www.nrcc.cornell.edu/wxstation/ithaca/ithaca.html).

To further examine lay date variability within individual females, we estimated intra-individual repeatability of lay dates using the *rpt* function in the *rptR* package in R v.3.5.1 (Stoffel et al. 2017, R Core Team 2018). We carried out one repeatability analysis on all

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446 breeding attempts and a second repeatability analysis on all breeding attempts undertaken by
447 older females.

448 RESULTS

449 Our final dataset included 1576 nesting attempts (1479 first nesting attempts and 97
450 second or renesting attempts) carried out by 867 females between 2002 and 2016. The average
451 lifespan of a breeding female swallow in our population was 1.7 years (range: 1-10 years). The
452 average number of fledglings produced during a female's lifetime was 4.9 (range: 0-39).
453 Initiation of breeding for yearlings was later on average than for older females (yearlings: 20
454 May vs older females: 14 May), though variation for both age classes was substantial (yearlings:
455 range 4 May – 24 June, older females: range 2 May – 20 June). In general, a female's first nest in
456 a season was most often initiated between 10 and 20 May (Figure 1).

457 *Relationship between lay date and older female fitness metrics.* Our best supported model
458 explaining variation in older female *clutch size* included the absolute lay date of each female's
459 current attempt ($R^2 = 0.48$), and revealed that females laying earlier in the year laid larger
460 clutches than did females who laid eggs later ($P < 0.0001$; Table 4, Appendix S1: Table S1).
461 *Clutch size,* in turn, strongly influenced variation in *number fledged* ($P < 0.0001$, Table 4,
462 Appendix S1: Table S3). In contrast, variation in lay date did not significantly influence directly
463 either *fledging success* (null model: $R^2 = 0.07$; Table 4, Appendix S1: Table S2) or *number*
464 *fledged* (null model: $R^2 = 0.20$; Table 4, Appendix S1: Table S3). However, lay date did strongly
465 influence *nestling mass*: earlier-reared nestlings were heavier than nestlings fledged from nests
466 initiated later in the season (current absolute date: $R^2 = 0.46$, $P = 0.02$; Table 4, Appendix S1:
467 Table S4). Our best-supported models explaining variation in older female *return rate* indicated
468 that a female's lay date in the previous year was associated with her likelihood of returning to the
469 study area in the following season (previous relative date: $R^2 = 0.16$; previous absolute date: $R^2 =$
470 0.15; Table 4, Appendix S1: Table S5). In this analysis, models fitted with a quadratic predictor
471 outperformed models fitted with only a linear effect of previous lay date, indicating that the
472 relationship between previous lay date and future return was curvilinear in nature – that is, that
473 the likelihood of future return for older females increased more than linearly with later lay dates
474 in the previous season (for previous relative date, quadratic $P = 0.002$ and linear $P = 0.009$; for
475 previous absolute date quadratic $P = 0.005$ and linear $P = 0.02$; Figure 2). Note that the effect

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being detected here manifests across three years: older females breeding early in 2010 would be expected to have a lower return rate not in 2011 but in 2012. Thus, these effects of laying date on return are not simple direct effects on death or dispersal but delayed until after the following breeding season. The very same effect appears in the MARK analyses (Appendix S1: Table S16).

Relationship between lay date and yearling fitness metrics. As for older females, *clutch sizes* for yearling females were strongly influenced by the absolute lay date of the current attempt ($R^2 = 0.12$; Table 4, Appendix S1: Table S6). Interestingly, a model that included a quadratic term outperformed one that included only a linear fixed effect of lay date, and indicated that *clutch sizes* were greatest for females laying at intermediate times (for current absolute date, quadratic $P = 0.009$ and linear $P = 0.83$; Figure 3). Lay date had no effect on either yearling *fledging success* (null model: $R^2 = 0.06$; Table 4, Appendix S1: Table S7) or *number fledged* (null model: $R^2 = 0.12$; Table 4, Appendix S1: Table S8). However, *clutch size* once again exerted a strong positive effect on *number fledged* ($P < 0.0001$, Table 4, Appendix S1: Table S8). In contrast to chicks fledged by older females, *nestling mass* in yearling nests did not depend on lay date (null model $R^2 = 0.28$; Table 4, Appendix S1: Table S9). Lay date also had no effect on yearling female *return rate* (null model: $R^2 = 0.10$; Table 4, Appendix S1: Table S10).

Relationship between lay date and lifetime reproductive output. There was a weak but statistically significant positive effect of yearling lay date on a female's *lifetime fledging success* (for yearling absolute date, $P = 0.01$, $R^2 = 0.06$; Table 4, Appendix S1: Table S11; for yearling relative date, $P = 0.02$, $R^2 = 0.07$, Table 4, Appendix S1: Table S11). Although this indicates that yearlings laying later may be more likely to be successful at least once in their life, another indicator of reproductive strategy, *average clutch size,* had a much stronger effect ($P < 0.0001$, Appendix S1: Table S11). Among females that fledged at least one nestling in their life, any advantage of later yearling lay dates is overshadowed by the advantages of earlier laying otherwise, as our best-supported model revealed that females whose average absolute lay date was earlier produced a greater number of fledglings overall (for average absolute date, $R^2 = 0.40$, $P < 0.0001$; Figure 4; Table 4, Appendix S1: Table S13). In this model, as for per-season *number fledged*, average *clutch size* was again positively related to *lifetime number fledged* (*clutch size*: $P < 0.0001$).

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Relationship between lay date and offspring recruitment. Our best-supported models indicated a significant effect of lay date, such that nestlings fledged from earlier nests were more likely to return to the study population as adults (for absolute date, $R^2 = 0.05$, $P = 0.04$; and for relative date, $R^2 = 0.05$, $P = 0.02$; Figure 5; Table 4, Appendix S1: Table S15).

Mother-daughter comparisons and repeatabilities. Our model for absolute lay date variation in 113 pairs of mothers and daughters revealed a significant positive effect of the mother's yearling lay date on that of her daughter (full model $R^2 = 0.36$; mother yearling lay date $P = 0.009$; Figure 6). In contrast, neither temperature during development nor temperature immediately prior to the yearling breeding attempt had any effect on the daughter's yearling lay date (natal temperature $P = 0.97$; breeding temperature $P = 0.35$). A similar analysis carried out on the lay dates of 32 mother-daughter pairs for which we had information on lay dates of mother-daughter pairs in their second breeding year failed to find any significant predictors of second-season lay date among these same factors (full model $R^2 = 0.33$; maternal lay date $P = 0.67$; natal temperature $P = 0.70$; breeding temperature $P = 0.36$). Intra-individual repeatability of absolute lay date among all females represented in our study was 0.15 (CI: 0.08-0.22, $P < 0.0001$). Intra-individual repeatability of absolute lay date among all older females represented in our study was 0.34 (CI: 0.23-0.44, $P < 0.0001$). We performed all the same analyses for relative lay date, and the results are consistent with those for absolute lay date, though the patterns are weaker (Appendix S1: Tables S17, S18 and associated text).

DISCUSSION

One limitation of past studies that have investigated the relationship between lay date and fitness is that this relationship has often been considered solely in the context of a single breeding season. That work has taught us a great deal about the seasonal decline in reproductive output and the linkage between clutch size and lay date (Verhulst and Nilsson 2008), but little about how it relates to longer-term breeding performance and survival of individuals. Our study looked beyond a single breeding season and followed individual female tree swallows throughout their lives, monitoring all measurable fitness components throughout. By taking such an approach, we were able to discern between two fundamental hypotheses about the nature of life history differences among individuals. Before proceeding to those hypotheses, we emphasize that the fitness effects of lay date variation are strongly intertwined with the effects of *clutch*

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size. Given all that has been done on the clutch size - lay date connection in tree swallows (e.g., Winkler and Allen 1996, Wardrop and Ydenberg 2003, Dawson 2008, Winkler et al. 2002, 2014), it came as no surprise that some of the effect of lay date on *number fledged,* both per-season and over the lifetime, was indirect: *clutch size* was strongly influenced by lay date throughout (Appendix S1: Tables S1, S6), but, though *clutch size* remained a strong predictor of number fledged in all relevant models (Appendix S1: Tables S3, S8, S13), in two of these (Appendix S1: Tables S3, S8), lay date did not add significantly to the explanatory power of *clutch size*, alone. Still, in the remaining model, lay date retained a strong direct connection to *lifetime number fledged*, and its variation was shown to have effects on many other aspects of the life history. We now review these other effects and discuss future research directions as they relate to understanding the costs and benefits of early breeding in tree swallows and the sources of individual variation in this key life history trait.

Quality vs. Alternative Strategies, yearlings vs. older females. Our results strongly suggest that earlier breeding tree swallows are of higher phenotypic quality than their late-breeding counterparts: in general, the relationships between reproductive performance and lay date were those predicted by an over-riding importance of individual quality, not the expression of alternative life history strategies (Table 4). In our population, earlier breeding was associated with larger *clutch size* and thus higher per-season *number fledged*, and in the nests of older females, broods from earlier in the season produced higher average *nestling mass* than did later nests. When we examined *lifetime number fledged*, earlier-breeding females fledged significantly more offspring, and the offspring fledged from such nests were more likely to recruit into their natal population as adults. Taken together, these results provide strong evidence that earlier breeding has higher fitness.

Interestingly, the associations between lay date and fitness that we observed were universally more pronounced among experienced breeders. This may indicate that inexperienced yearlings in our population are less savvy in successfully navigating the costs and benefits of breeding at a particular time. In a population of breeding tree swallows in Wisconsin, there was evidence that yearlings were less adroit in managing their mating choices: experienced females mated with more extra-pair sires when paired with a genetically similar mate, and broods that had more sires exhibited greater hatching success. In contrast, inexperienced females did not

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adjust their mating behavior according to their genetic similarity to their mate and thus missed out on a potential benefit of polyandry (Whittingham and Dunn 2010). Wearing a distinctive brown plumage, yearlings may also be less attractive to prospective mates, delaying their formation of a pair bond (cf. Bitton et al. 2008, Coady and Dawson 2013, Taff et al. 2019). Both of these factors could help explain why reproductive output is consistently lower among yearlings in our population.

Of all of the fitness metrics that we examined in yearlings, the two that were most affected by lay date variation were also the only two metrics in our entire study that exhibited a negative quadratic relationship with lay date. Both *clutch size* and, indirectly, *number fledged* tended to be highest among yearlings breeding at intermediate times – both were reduced in the earliest and the latest breeders. This strengthens the indication that yearlings are more sensitive to costs of early breeding while being unable to take advantage of some of its benefits. Indeed, all of these indications of the advantage of yearling delay may have exerted selective pressures toward less attractive brown yearling plumage. In any event, it appears that females are likely subject to selection on lay date that varies in direction and mode across their lifespans (see also Tarwater and Arcese 2017).

This difference between yearlings and older females in the effects of lay date may be behind the one result for older females that runs counter to the Quality Hypothesis: among older females, the likelihood of returning one year later was higher among those individuals whose previous breeding attempt had taken place *later* in the season (Figure 2, Table 4, Table S5). In this result, we see evidence that later breeding may confer a survival advantage, consistent with the idea that some females may forgo reproductive benefits of early breeding to invest more heavily in self-maintenance and future survival. This result is one of the weakest significant results in this study ($R^2 = 0.16$), and, though current female age was included in the two best supported models, the coefficient for current age was not significant in either one ($P > 0.18$). The average lifespan of female tree swallows included in this study was 1.7 years. Thus, the typical female did not make it past a single breeding season, and the sample of older females in Table S5 is dominated by older females in their first post-yearling breeding season. In this case, we cannot suggest other biological mechanisms that might explain a delayed trade-off in costs, and we tentatively ascribe most of this effect to the difference between yearlings and older females in

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their breeding life histories. The strong ($R^2 = 0.40$) overall prediction of total *lifetime number fledged* in our study came from a simple linear relationship with mean absolute lay date of the female (Appendix S1: Table S13).

The relevant time scale of lay date effects. In every instance in which we observed a positive association between early breeding and female performance, that association indicated an effect of the lay date on the female's current attempt. In contrast, we only observed two negative associations between early breeding and female performance: the one just discussed indicating an effect of current lay date on a female's return rate two years hence and the finding that later-laying yearlings had higher *lifetime fledging success* (Appendix S1: Table S11). These two negative effects are both quite weak ($R^2 < 0.15$), and the large number of positive associations between earlier lay date and reproductive performance indicate that its benefits are generally short-lived and limited to the current breeding season. Previous research has concluded that tree swallows are income breeders – that they acquire the resources necessary for breeding in the days immediately before breeding begins (Winkler and Allen 1995, Nooker et al. 2005). The results of this study indicate that, in the same time horizon that resources are acquired and invested, most of the costs of those allocations are being paid.

Mother-daughter similarity and repeatability. Lay date had a significant repeatability coefficient in female tree swallows, a result that would be expected under the Quality Hypothesis. But the finding that a female's yearling lay date was significantly influenced by the yearling lay date of her mother suggests that an important aspect of individual quality differences may stem from genetic or maternal effects. Surprisingly, we found no evidence that temperatures during development or immediately prior to breeding influenced a female's yearling lay date. Past research in tree swallows has documented population-level advancements in laying date in concert with warmer spring temperatures, suggesting that environmental conditions immediately prior to breeding are important determinants of lay date at the population level (Dunn and Winkler 1999, Hussell 2003, Shipley et al. & Winkler et al. in prep.). However, our results suggest that individual-level determinants of lay date may involve a more complex suite of factors. In fact, when we examined determinants of older female lay date among the 32 mother-daughter pairs for which we had information on lay dates from attempts in their second breeding seasons, we found no significant determinants of lay date among those factors that we investigated. At the same time, lay date repeatability was greater among older females than

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among all females, suggesting that the individual signature of lay date becomes stronger as females age. It is also interesting that individual repeatabilities in absolute lay dates were higher than those for relative lay dates. Of the 13 models in Appendix 1 with a significant effect of lay dates, 3 included both absolute and relative lay date measures in the best supported models, 5 had only absolute lay dates as predictors in the best supported models, and none had relative lay dates alone. This suggests, as in another study of tree swallows (Bourret et al. 2015), that social factors are not as important as we suspected in determining lay dates. Surprisingly, the majority of the response to environmental factors appears to come from individual responses to photoperiodic and other year-invariant factors. In the future, it will be important to understand exactly what factors cause a female swallow to breed at a particular time (cf. Bourret et al. 2015), as well as how the potential decline in maternal influence across the lifespan influences opportunities for a response to selection on lay date to occur.

Potential for response to selection. Tree swallows continent-wide have been shifting their lay date earlier (Dunn and Winkler 1999); however, evidence for a comparable advance in lay dates in single sites with long records of monitoring is much weaker or non-existent (i.e., Hussell 2003, cf. Shipley et al. in prep.). If earlier breeding generally results in better fitness outcomes, why then do we not see ever-advancing lay dates in response to strong directional selection? Price et al. (1988) modeled such a lack of selective advance in lay date in the face of directional selection as resulting from constraining correlations between physiological condition and lay date. However, Winkler and Allen (1995, 1996) showed that, though female tree swallows achieve good condition before they lay, they are not laying eggs on somatic stores of resources that they brought with them on migration, and thus, the condition of early spring birds is not determining their lay dates.

Our data suggest that older females are under strong directional selection for earlier laying and that yearlings are under balancing selection to breed early, but not *too* early. At the same time, lay dates among yearlings were determined at least partly by that of their mothers, while lay dates among older females were not. Thus, yearling lay date may be partially heritable and able to respond to the balancing selection that such females face, while older female lay date appears to be responsive to more varying environmental factors and thus less heritable and less likely to respond to any form of selection, however strong. At a population level, these patterns

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may result in a continuous stream of young birds suffering reproductive deficits for breeding too early, leading to the production of offspring which are primed to breed later as yearlings. As such females age, they may breed earlier to great advantage, but this early breeding is unlikely to transfer into the next generation of swallows.

Generalizing to other members of the population, "invisible fractions" and beyond. Our goal was to examine the relationships between lay date and various fitness components over the course of a swallow's entire life, thus limiting our analyses to including swallows for whom we had complete information regarding their reproductive histories. In limiting our analyses in this way, we excluded members of the population whose relationship to lay date could be markedly different.

First, we excluded from analysis any females that did not breed in our population as yearlings. Approximately 40% of the females that enter our population do so in older female plumage. Although we do not know what, if any, breeding activities they engaged in prior to their initial breeding effort in our study area, their numerical abundance means that it is important to consider whether they are likely to differ in behavior from females who bred in our study area for the first time as yearlings. This seems most likely to be the case if these unbanded older females spent their adult life prior to their first breeding effort at our sites as non-reproductive floaters. The alternative is that such females might have bred elsewhere before moving into our study area. While we cannot definitively account for the behavior of unbanded older females prior to their entry into our population, their *clutch size*, brood size, and *number fledged* in their first year in our study area are indistinguishable from those of older females that first bred in our study area as yearlings. In fact, the only point of dissimilarity is that older females breeding in our population for the first time lay earlier than yearlings but later than older females with prior breeding experience on our study sites (D.W. Winkler, unpublished data). Taken together, these results suggest that most females entering our study area in older female plumage have bred elsewhere in the past, and their later-than-expected lay dates perhaps reflect additional costs involved in adjusting to an unfamiliar site and a new mate or adjusting a response mechanism that may have been tuned to a previous breeding site. In the future, it will be important to consider whether such costs materially shift the intricate balance of benefits and costs associated with variable lay date and, if so, how this might affect the population's ability to

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687 adapt to changing environmental conditions. Additionally, several other populations of tree
688 swallows exhibit different compositions of yearlings and older females. For example, a long-
689 term study area in Wisconsin encounters nearly 90% of its females for the first time in older
690 female plumage (Whittingham and Dunn 2010). Understanding how lay date affects fitness in
691 populations that exhibit different demographic structure should become a priority for future
692 research.

693 Our finding that earlier-breeding females were less likely to return to our study area two
694 years hence lends support to the idea that early breeding can impair future survival in the subset
695 of individuals that already are living longer than most. However, as in any discussion of a
696 segment of a bird population that disappears between seasons, these results could also indicate
697 that earlier-breeding birds may have been more likely to disperse to a new breeding site two
698 years later. Tree swallow females in this population are site-faithful 86% of the time, and
699 breeding females are more likely to disperse following a reproductive failure (Winkler et al.
700 2004). It is possible that early-breeding yearlings, more likely to fail, are also more likely to
701 disperse away. Not being able to follow this "invisible fraction" (cf. Grafen 1998) may thus give
702 us a biased interpretation of the importance of lay date.

703 Our study also did not consider the relationship between lay date and performance in
704 male tree swallows. Male reproductive output is inherently more challenging to measure because
705 of the high rates of extra-pair paternity in this species (reviewed in Winkler et al. 2011). Not only
706 does accurate assessment of male siring success require complete genotyping of the population,
707 but the gregarious nocturnal roosting behavior of this species early in the season may create the
708 opportunity for males to routinely sire offspring in nests that are located well outside of the focal
709 study area (see Dunn and Whittingham 2005, Stapleton and Robertson 2006). Nevertheless, the
710 relationship between timing of breeding and male performance is worthy of future attention, both
711 in its own right and because males may materially affect when females choose to breed and how
712 successful they are when they do.

713 If we extend the scope of generalization to other populations of the same species (e.g.,
714 Wardrop and Ydenberg 2003, Dawson 2008, Harriman et al. 2017), the results we report here
715 can be seen to depend on the environments to which the same bird species is exposed. Wardrop
716 and Ydenberg (2003) reported support for both quality and date effects in a hatch-date

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717 manipulation in British Columbia. Dawson (2008) conducted a similar experiment and reported
718 that, despite complicating effects of inclement weather, the date effects was better supported at
719 another site in the same province. Harriman et al. (2017) conducted paired experiments in both
720 British Columbia and Sakatchewan over two seasons, and concluded that declines in food
721 availability with date were most important in affecting seasonal reproductive declines. Such
722 declines in seasonal food availability contrast with those elsewhere in the species' range,
723 including the Ithaca field sites (Dunn et al. 2011). Tree swallows clearly have a life history that
724 is able to flexibly respond to variable conditions in both space and time.

725 The lifetime perspective developed here has allowed us to extend the scope of fitness
726 consequences beyond single breeding seasons, and the lay date effects we have seen on *offspring*
727 *recruitment* and *lifetime number fledged* mirror those detected in another well-studied swallow
728 (Saino et al. 2012, Raja-Aho et al. 2017, cf. Evans et al. 2019).

729 *Conclusions and perspective.* In the context of the hypotheses laid out in the beginning of
730 this paper, it appears that most of the variation in breeding phenology and its consequences are
731 due to variation in the overall phenotypic quality of females and not alternative life history
732 strategies being traded off differently among individuals. In many ways, these results reinforce
733 much of what has been known or suspected about tree swallows for decades – that they are
734 income breeders whose performance is tied to contemporary environmental factors that must be
735 'just right' in order for successful reproduction to occur, that earlier breeders are of superior
736 quality to their later-breeding counterparts, and that timing of breeding is one of the most
737 important determinants of tree swallow reproductive output. But in other ways, this study yields
738 new insight that provokes a whole host of unanswered questions. Are there combinations of
739 ecological factors that might make later breeding the more favorable strategy, and if so, what
740 would they be? The contrast in the life histories of yearling vs. older females, and the presence of
741 maternal effects on yearling lay dates, suggest many interesting research challenges for better
742 understanding the lives of yearling breeders and how the reproductive challenge changes for
743 those that survive to breed as older females. And finally, given that lay date seems so
744 fundamental to tree swallow fitness, what are the actual mechanisms by which a female swallow
745 decides to start laying on a given date? Answering these questions and others will help future

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researchers better understand this important and often enigmatic life history trait in a well-studied bird.

This study's results are interesting from much broader perspectives as well. The timing of breeding is probably the life history trait that has borne the clearest signal of climate change impact across the broadest range of taxa, and the fact that, in this relatively short-lived vertebrate, non-genetic quality differences are the prevailing influence on this critical life history trait might engender some hope for the future of this and other vertebrate populations. Even though there may be some heritable basis for lay date variation, it is clear that these small birds have ample means for adjusting their timing of breeding throughout their lives and this life-long flexibility suggests an on-going responsive adjustment to the rapidly changing anthropogenic environments around them. The Ithaca tree swallow population can most accurately be seen as being made up of individuals, each with a similar tool kit for meeting environmental and developmental challenges, varying in their fitness because of chance variations in the conditions that each individual encounters in their ontogeny and ecology through each of their lives.

ACKNOWLEDGMENTS

Kelly Hallinger and David Winkler contributed equally to this work and served as co-principal authors. We thank the many dozens of undergrads and visitors who helped us monitor and amass the data in this paper. This research was supported by NSF IBN-0131437, DEB-0717021, and DEB 1242573 to DW Winkler, by NSF IOS-1457251 to MV, and by undergraduate support from Cornell University. All work reported here was conducted under Protocol number 2001-0051 approved by Cornell University's IACUC.

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Data Availability

Data are available from The Knowledge Network for Biocomplexity (KNB) at: https://doi.org/10.5063/F1NP22S4.

TABLE 1. Fitness metrics under examination, along with an explanation of fixed and random effects included in each model. Plus and minus signs under H1 and H2 refer to the predicted relationship between lay date and each fitness metric if timing of breeding reflects variation in individual quality (H1) or if it reflects the expression of alternative life-history strategies (H2).

	Fitness metric	Definition	Fixed effects	Random effects	H1	H2
Offspring quantity	*clutch size*	maximum number of eggs observed in first nest each season	lay date	female identity, hatch year, current year, current site	-	-
	fledging success	binary 0-1 indicator of whether a female fledged any young in a given season	lay date, *clutch size*	female identity, hatch year, current year, current site	-	-
	number fledged	number of nestlings fledged from a female's successful nest(s) over entire season	lay date, *clutch size*	female identity, hatch year, current year, current site	-	-

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Offspring quality	*nestling mass*	average mass of all nestlings in brood that would later go on to fledge	lay date, age of nestlings at measurement, *number fledged*	female identity, hatch year, current year, current site	-	+
	fledgling recruitment	binary 0-1 indicator of whether fledgling ever reappeared in study area as adult	maternal lay date, maternal age class	nest identity, natal year, natal site	-	+
Adult survival	*return rate*	binary 0-1 indicator of whether adult was detected in study area in any subsequent year	lay date, *fledging success*	female identity, hatch year, current year, current site	-	+
Lifetime fitness	*lifetime fledging success*	binary 0-1 indicator of whether a female fledged any young over the course of her life	lay date, average *clutch size*	hatch year	-	+/-
	lifetime number fledged	number of fledglings believed to have been fledged by a successful female's nests in her lifetime	lay date, average *clutch size*	hatch year	-	+/-

1 TABLE 2. Explanation of lay date variants tested in alternative candidate models.

	Lay date variant	Definition	Interpretation
Time scale over which timing of breeding exerts effects	yearling	earliest clutch initiation date during yearling year	organizational effect of first breeding effort
	current	earliest clutch initiation date during current year	short-term effect

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	previous	earliest clutch initiation date during previous year	long-term effect
Importance of social context in mediating timing of breeding effects	absolute	date defined as 1 = 1 May	effects independent of social context
	relative	date defined as 1 = earliest clutch initiation during current season	effects dependent on social context
Potential for timing of breeding to respond to selection	linear	performance exhibits monotonic increase or decrease with advancing lay date	directional selection on timing of breeding
	quadratic	performance exhibits parabolic relationship with advancing lay date	stabilizing selection on timing of breeding

TABLE 3. Variables under examination in analysis of causes of lay date variation.

Fixed effect	Definition	Interpretation
mother's lay date	mother's absolute clutch initiation date (1 = 1 May)	genetic or maternal effects contribute to variation in lay date
natal environment	average daily max temperature calculated from lay date + 41 days (approximate fledging date)	developmental environment contributes to variation in lay date

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yearling environment	average daily max temperature from 16-30 April	contemporary environment contributes to variation in lay date	

TABLE 4. Summary of best-supported model(s) for each fitness metric under examination. Plus signs under H1 and H2 refer to support for the predicted relationship between lay date and each fitness metric if timing of breeding reflects variation in individual quality (H1) or if it reflects expression of alternative life history strategies (H2).

	Fitness metric	Shape of effect	Timing of effect	Scaling of effect	Direction of effect	H1	H2
Offspring quantity	*clutch size*	linear (older females), quadratic (yearling females)	current	absolute	-	-	-
	fledging success	none	none	none	none	-	-
	number fledged	none	none	none	none	-	-
Offspring quality	*nestling mass*	linear	current	absolute	- (older females), none (yearling females)	-	+
	fledgling recruitment	linear	current	absolute/relative	-	-	+

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Adult survival	*return rate*	quadratic	previous	absolute/relative	+ (older females), none (yearling females)	-	+
Lifetime fitness	*lifetime fledging success*	linear	yearling	absolute/relative	+	-	+/-
	lifetime number fledged	linear	average	absolute	-	-	+/-

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FIGURE LEGENDS

FIGURE 1. Distribution of tree swallow absolute lay dates (n = 1479 breeding attempts).

FIGURE 2. Relationship between absolute lay date in previous year and likelihood of future return (n = 493 breeding attempts). Solid line indicates average *return rate* for females predicted by linear model of female return on lay date in previous year. Dashed line indicates average female *return rate* predicted by model including a quadratic effect of lay date in previous year. Sample sizes are displayed above each point. For interpretation see text.

FIGURE 3. Relationship between absolute lay date in current year and *clutch size* for older female and yearling female attempts (n = 612 older female attempts and n = 867 yearling attempts). Points represent mean *clutch size* produced by females whose absolute lay date fell within each of eight one-week intervals. Bars represent standard errors, and sample sizes are above each point.

FIGURE 4. Relationship between average absolute lay date and *lifetime number fledged* for females that fledged at least one nestling (n = 616 females). Points represent mean number of fledglings produced by females whose average absolute lay date fell within each of seven one-week intervals. Bars represent standard errors, and sample sizes are above each point.

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FIGURE 5. Relationship between a fledgling's absolute lay date and its likelihood of recruiting as a breeder in the Ithaca study population (n = 3205 fledglings). Sample sizes appear above each data point.

FIGURE 6. Relationship between absolute lay dates of mothers and daughters breeding in their yearling years. Solid line indicates the expectation if a daughter's lay date was completely determined by her mother's lay date (n = 113 mother-daughter pairs). For further details see text.

FIGURE 1

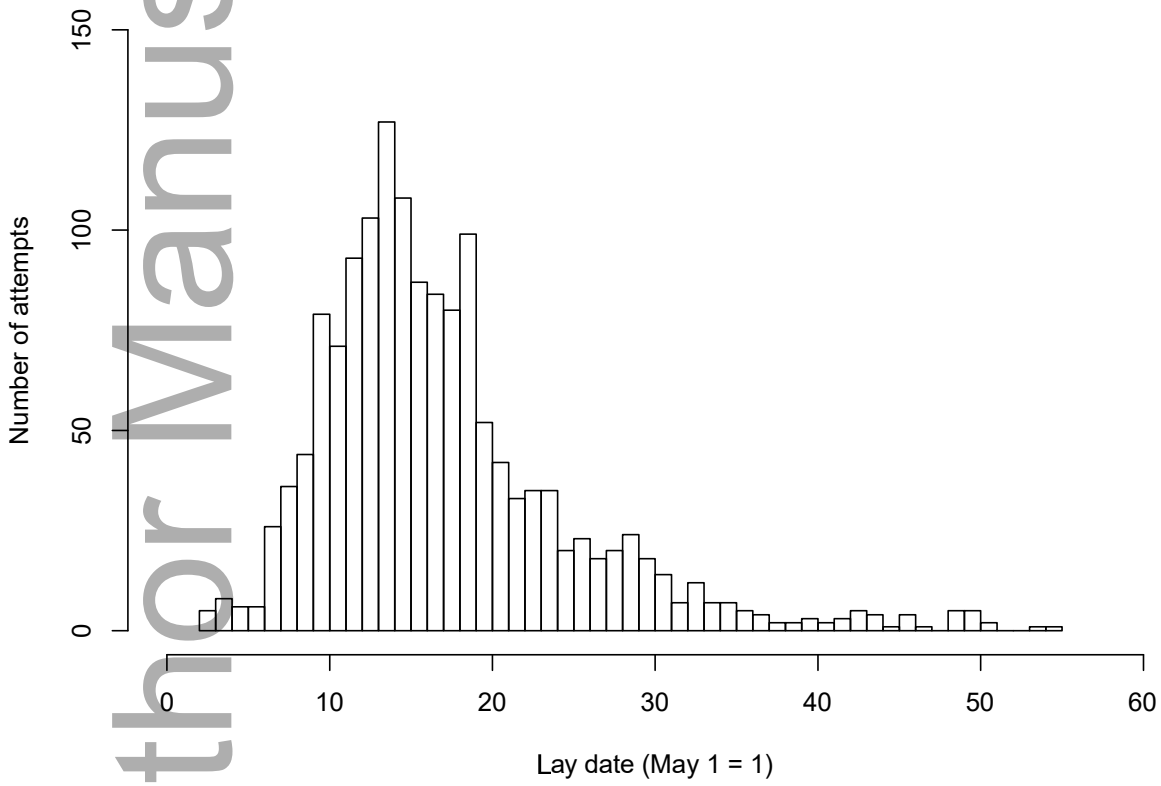

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FIGURE 2

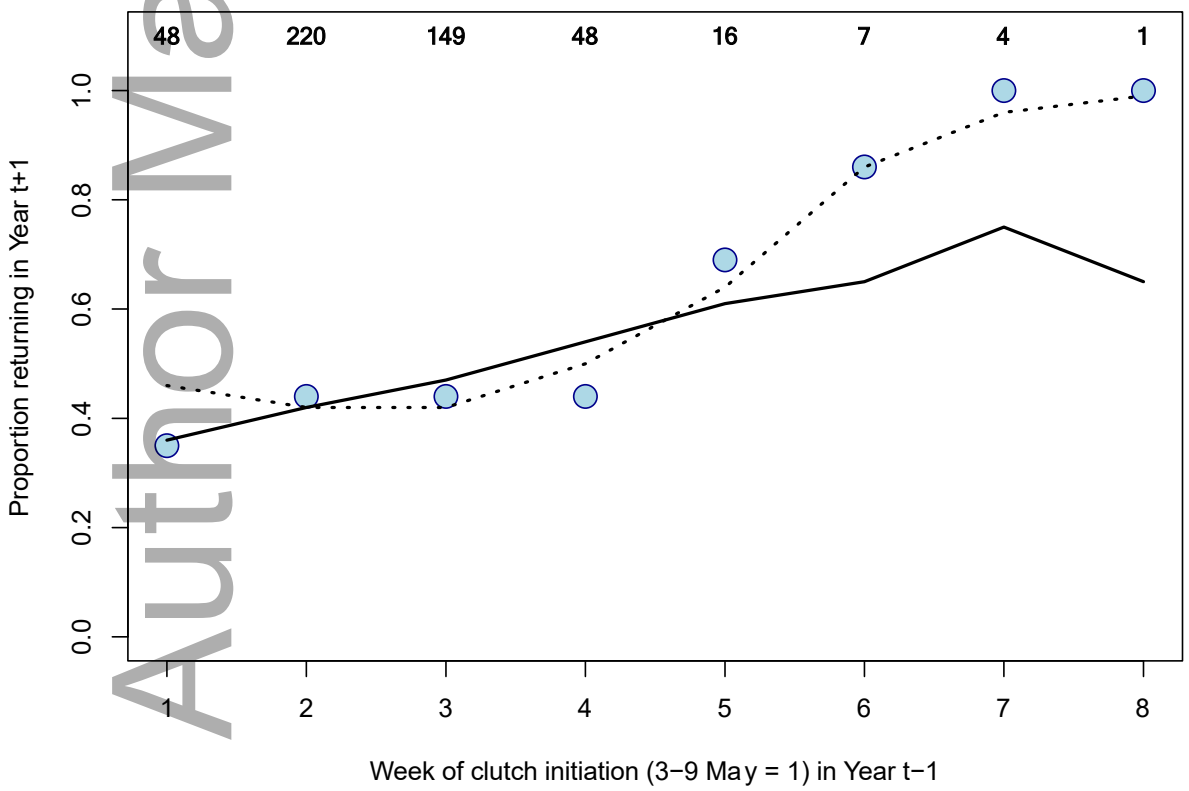

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FIGURE 3

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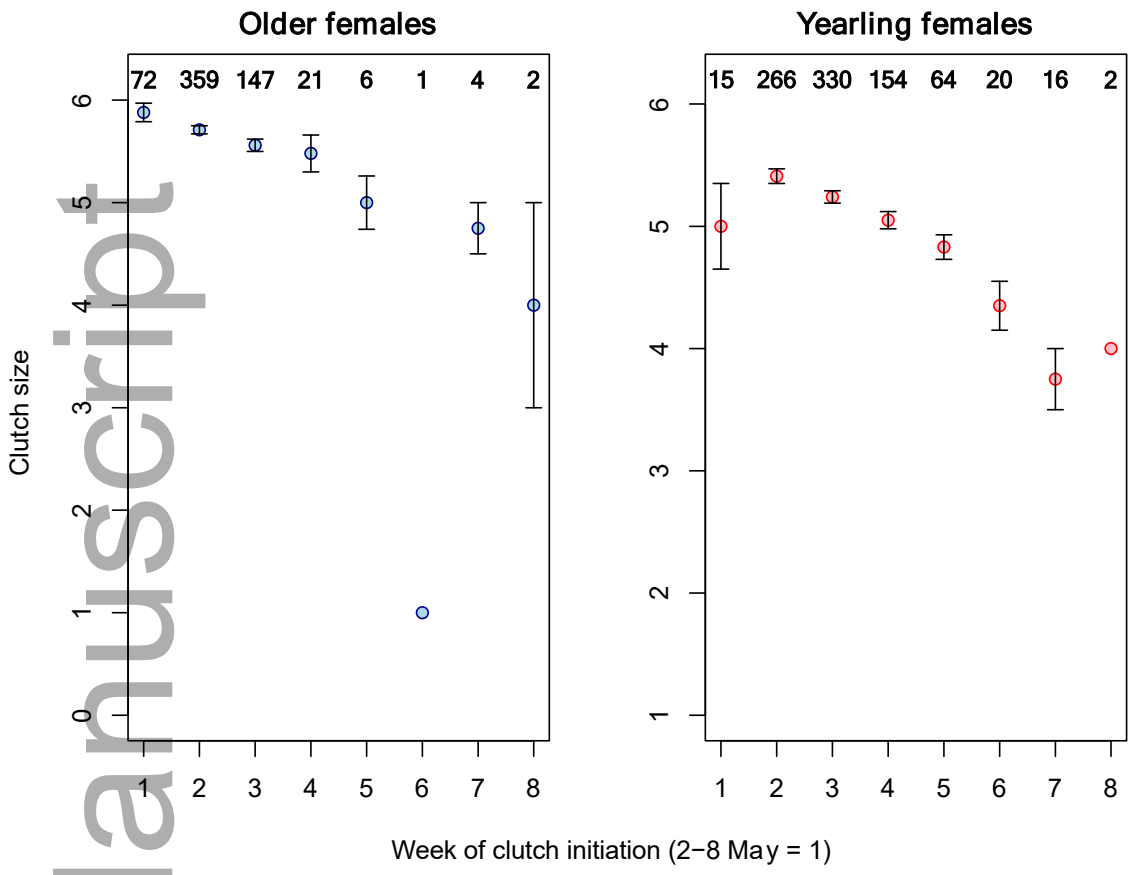

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FIGURE 4

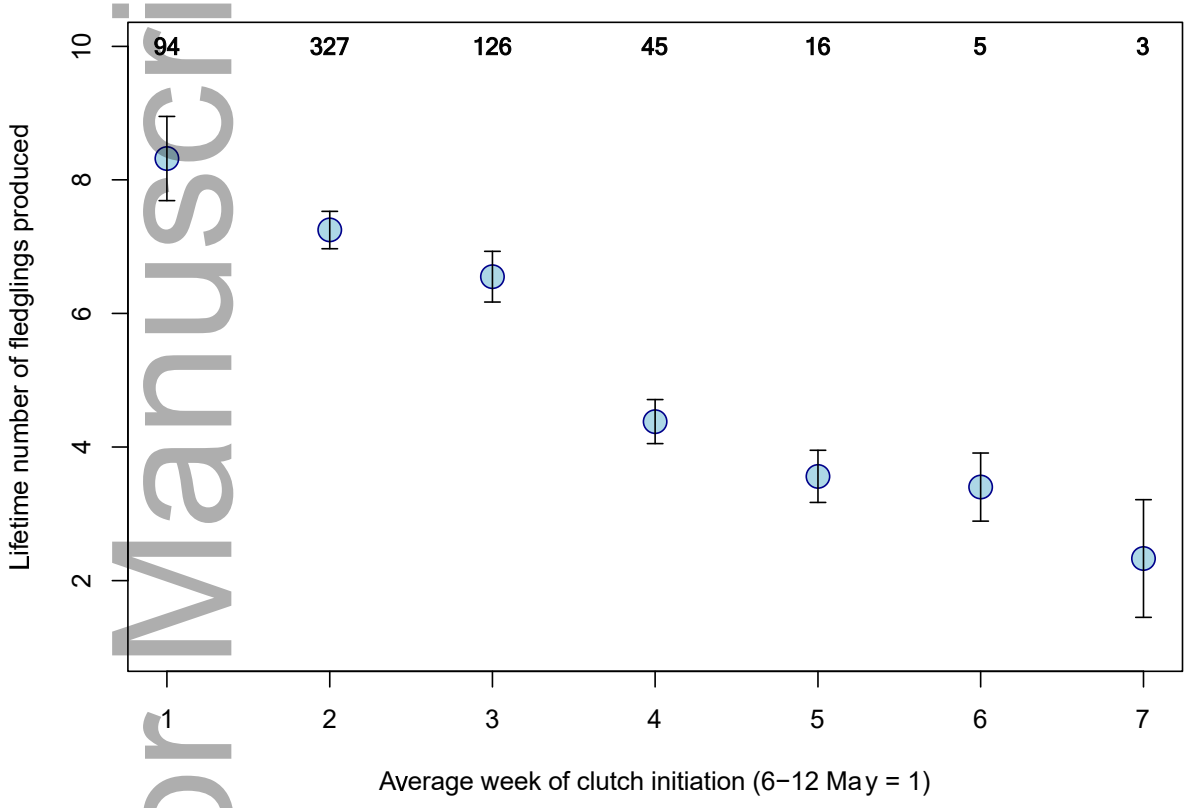

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FIGURE 5

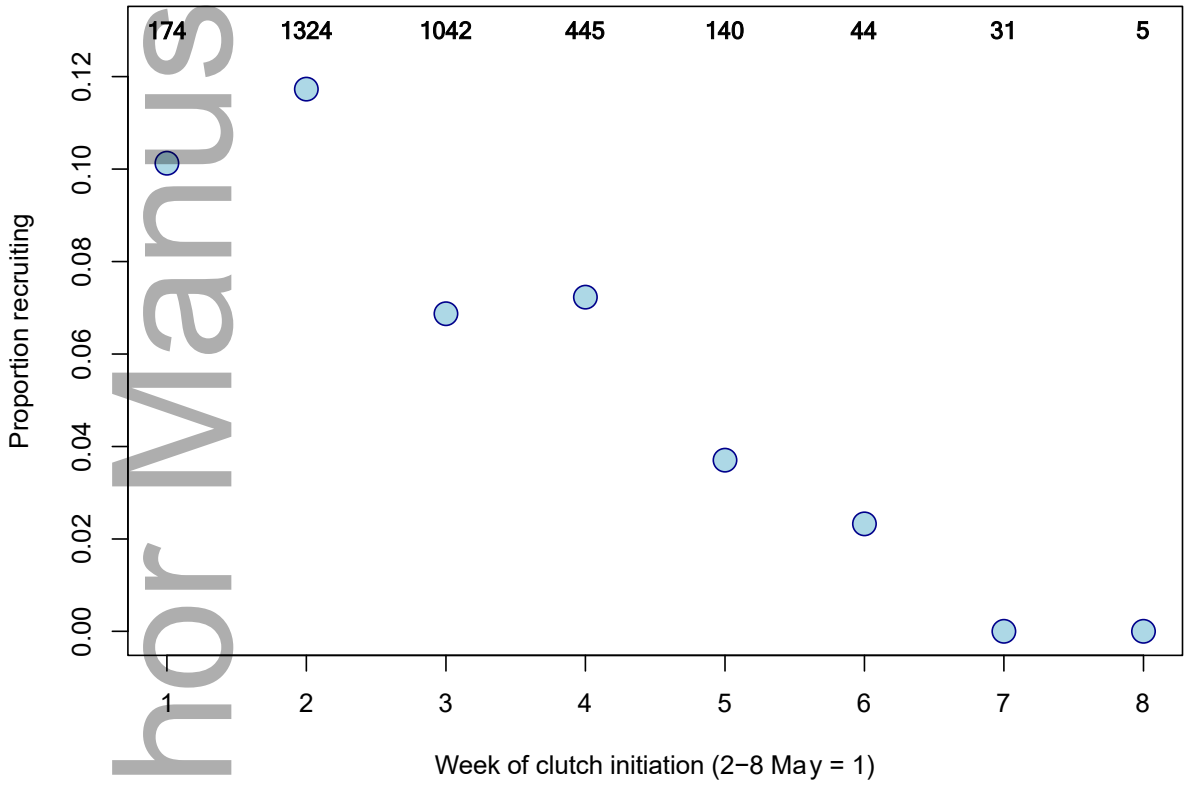

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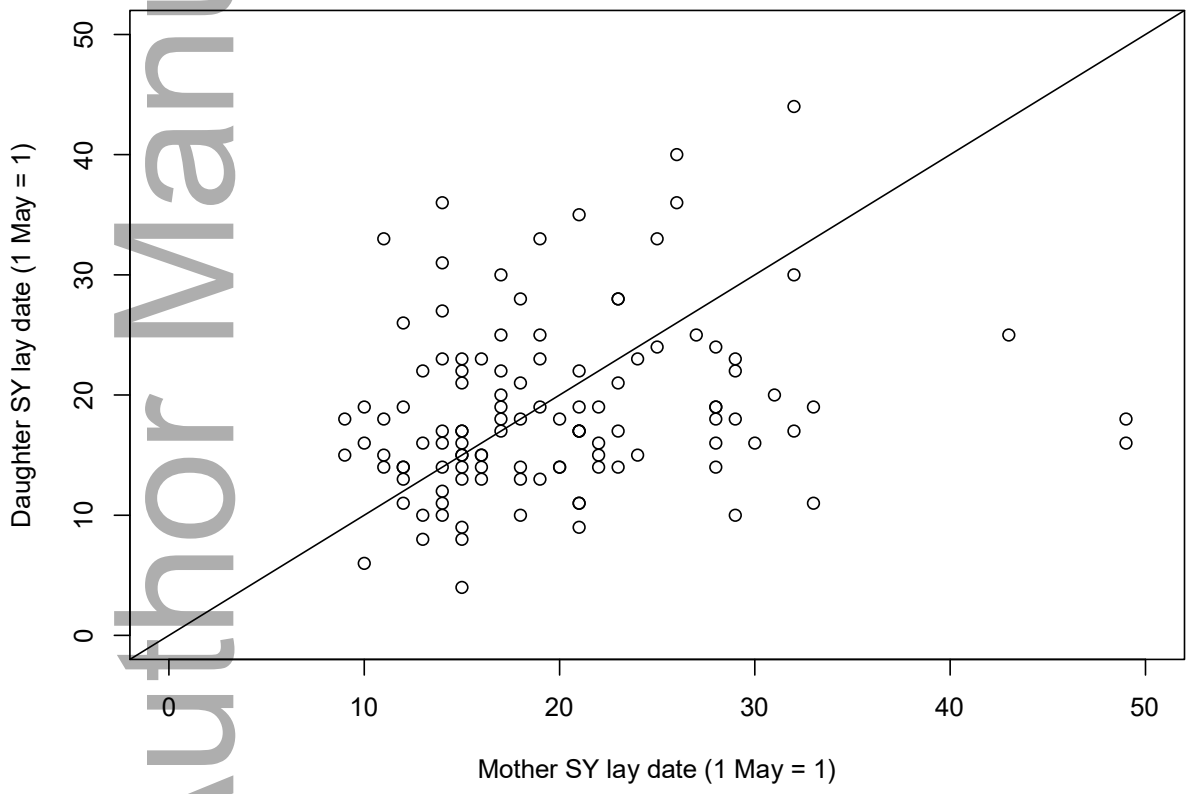
FIGURE 6



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