

# Timing of breeding and environmental factors as determinants of reproductive performance of tree swallows

Russell D. Dawson

**Abstract:** Decreased reproductive success among birds breeding later in the season is a common pattern in temperate environments, although the underlying mechanisms remain unresolved. The quality hypothesis suggests that high-quality individuals can begin breeding earlier in the season than poorer quality parents, and are also able to invest more in reproduction. Alternatively, the date hypothesis suggests that reduced success among late birds is due to some correlate of date, such as decreased food abundance or offspring value. To test these hypotheses, I manipulated the date that tree swallows, *Tachycineta bicolor* (Vieillot, 1808), raised offspring by swapping clutches among nests so that birds were raising young either earlier or later than intended, and compared reproductive performance with control nests. My results showed that fledging success was related to the date hypothesis, with later birds being less successful in raising offspring than early breeding birds. Size and mass of offspring were not explained by either hypothesis, but rather by weather conditions experienced prior to measurements being taken. My results highlight the importance of events such as periods of inclement weather that can have significant impacts on offspring quality independently of both date of breeding and parental quality.

**Résumé :** On observe couramment un succès reproductif réduit chez les oiseaux qui se reproduisent plus tard dans la saison dans les milieux tempérés, bien qu'on en connaisse pas les mécanismes sous-jacents. L'hypothèse de la qualité avance que les individus de haute qualité peuvent commencer à se reproduire plus tôt dans la saison que les parents de faible qualité et qu'ils peuvent aussi investir plus dans leur reproduction. L'hypothèse de recharge, celle de la date veut que le succès réduit chez les oiseaux tardifs soit dû à un facteur en corrélation avec la date, comme une diminution d'abondance de la nourriture ou de la qualité des rejetons. Afin de tester ces hypothèses, la date à laquelle des hirondelles bicolores, *Tachycineta bicolor* (Vieillot, 1808), élèvent leurs petits a été manipulée par des échanges de portées entre les nids de façon à ce que les oiseaux élèvent leurs petits plus tôt ou plus tard que prévu; leurs performances reproductives ont été comparées à celles de nids témoins. Mes résultats montrent que le succès à l'envol est relié à l'hypothèse de la date, selon laquelle les oiseaux plus tardifs ont moins de succès dans l'élevage de leurs petits que les oiseaux qui se reproduisent tôt. Ni l'une, ni l'autre des hypothèses n'explique la taille et la masse des rejetons qui sont plutôt reliées aux conditions climatiques dans la période qui précède les prises de mesures. Mes résultats soulignent l'importance d'événements tels que des périodes de conditions météorologiques inclementes qui peuvent avoir des impacts importants sur la qualité des rejetons, indépendamment de la date de la reproduction et de la qualité des parents.

[Traduit par la Rédaction]

## Introduction

In seasonal environments, declines in reproductive success among individuals that breed later in the season is a pervasive pattern exhibited by diverse taxa (e.g., Clutton-Brock 1988; Cushman et al. 1994; Spear and Nur 1994). This phenomenon has attracted a great deal of attention from ecologists and has been extensively studied in avian populations (reviews in Nilsson 1999; Arnold et al. 2004; Verhulst and Nilsson 2008). Declines in reproductive success with later breeding are the consequence of two processes. First, late-breeding birds often have reduced clutch and brood sizes, and so have reduced fecundity-dependent fitness (Svensson 1997). Second, later breeding is also associated with declines in fecundity-independent fitness, as late-

hatching offspring are often of poorer quality and may be less likely to survive to breeding age (Svensson 1997). Despite much empirical research on this subject, no consensus exists concerning the mechanism(s) underlying the processes that lead to reduced reproductive success among late breeders (Verhulst and Nilsson 2008).

Two of the most common hypotheses for seasonal declines in reproductive success are the "quality" and "date" hypotheses. The quality hypothesis suggests that seasonal changes in reproductive success are the result of differences in quality among individuals, such as phenotypic quality or body condition (Price et al. 1988; Verhulst and Nilsson 2008). The date hypothesis suggests that declines in reproductive success with later breeding are due to breeding date per se or some correlate of breeding date that affects all individuals equally. For example, systematic changes during the breeding season in food abundance or offspring value may alter reproductive success independently of parental quality (Bryant 1975; Daan et al. 1990). Although the quality and date hypotheses are not mutually exclusive (Verhulst et al. 1995), they do yield distinct predictions when breeding

Received 15 January 2008. Accepted 2 May 2008. Published on the NRC Research Press Web site at [cjz.nrc.ca](http://cjz.nrc.ca) on 17 July 2008.

**R.D. Dawson.** Ecosystem Science and Management, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada (e-mail: [dawsonr@unbc.ca](mailto:dawsonr@unbc.ca)).

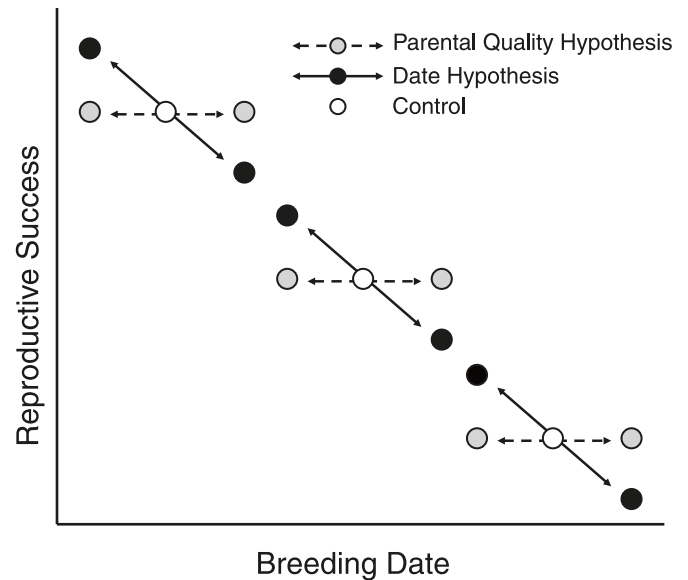
dates are experimentally altered. The date hypothesis predicts that performance of parents will be related to the date that parents are actually raising young as opposed to performance being related to the intended breeding date of the parents. In this scenario, parents that are manipulated into raising young early will have enhanced performance, while those forced to raise young later will have reduced success, compared with that which would be expected if they raised young at their intended time (Fig. 1). In contrast, the quality hypothesis predicts that because birds that initiate breeding earlier are superior, experimentally advancing or delaying hatching dates would not change performance; rather, success will be related to each pair's intended breeding date as opposed to actual breeding time. Therefore, parents whose breeding dates have been altered so that they are breeding earlier will do poorer, while those birds that are delayed will do better, compared with unmanipulated birds breeding at the same time (Fig. 1).

Perhaps one of the reasons that causes of declining reproductive success among later breeders remain controversial is the difficulty in experimentally manipulating timing of breeding, as it is not possible to alter timing of breeding in a direct manner (Verhulst and Nilsson 2008). One common method of delaying breeding is to remove first clutches, forcing females to lay a replacement clutch later in the season (e.g., Verhulst et al. 1995). Alternatively, some researchers have used a swapping protocol, whereby clutches initiated on different dates are exchanged among nests (e.g., Norris 1993). One advantage of clutch swaps is that it is possible to manipulate timing of breeding in both directions, forcing birds to breed both earlier and later than they had anticipated. Nonetheless, neither of these are "clean" manipulations (Verhulst and Nilsson 2008), as the former method requires birds to lay a replacement clutch, while the latter alters the period of incubation and evidence is accruing that this may be relatively costly (e.g., Heaney and Monaghan 1996; Reid et al. 2000; Wardrop and Ydenberg 2003). In this study, I tested the quality and date hypothesis using a clutch-swapping protocol to manipulate timing of breeding by tree swallows (*Tachycineta bicolor* (Vieillot, 1808)), a small insectivorous passerine. I compared performance of birds breeding both earlier and later in the season than they had intended with a group of control birds. I also included body condition of parents as a potential covariate in my analyses to control for any unintended effects on condition caused by the manipulation.

## Materials and methods

I studied tree swallows from May to July 2001 and 2002, in an area south of Prince George, British Columbia, Canada (53°45'N, 122°33'W). The area consisted of open agricultural fields, primarily hay field and pasture, interspersed with small wetlands, and surrounded by patches of deciduous and coniferous trees of varying sizes. Tree swallows arrived on the site in early May and began laying eggs in late May and early June. Swallows bred in nest boxes that were mounted on fence posts approximately 1.5 m from the ground and were spaced approximately 30 m apart. Nests were visited every 1–2 days beginning in mid-May, and then daily once egg laying had commenced, allowing me to

**Fig. 1.** Predictions of the quality and date hypotheses for causes of declining reproductive success associated with breeding later in the season. The quality hypothesis suggests that breeding date is a function of individual quality, with high-quality birds breeding earlier and having more resources available to invest in reproduction. Experimentally advancing or delaying hatching dates would not be expected to change performance; rather, success will be related to each pair's intended breeding date as opposed to actual breeding time. The date hypothesis predicts that declines in reproductive success with later breeding are the consequence of changes in the environment (e.g., food supply) that affect all birds equally. Success of birds with manipulated hatching dates will be similar to unmanipulated pairs raising young at the same time.



determine both clutch initiation date and clutch size. Once clutches were completed, nests with the same clutch size (range 5–7 eggs) were grouped into sets of four so that two of the nests were initiated on the same day, while the other two nests were initiated 4 days later. When the nests that were initiated earlier reached day 10 of incubation, I then swapped the clutch of eggs between one of the nests that was initiated earlier in the season with the clutch from a later nest. During the clutch-swap process, artificial eggs were placed in the nests to prevent parents from abandoning their breeding attempt. As a consequence of this manipulation, one set of parents in each group raised young 4 days earlier than they had anticipated ("early" nests), while another set of parents raised young 4 days later than they had expected ("late" nests). While 4 days is a relatively small alteration of breeding date, similar time spans have been used in previous manipulative studies (e.g., Norris 1993; Wardrop and Ydenberg 2003). In addition, in my study area 90% of nests were initiated over only a 14-day period in each year and so 4 days represents a considerable change in breeding time for tree swallows. The remaining two nests in each group then acted as controls for the early and late nests. Eggs in control nests were also removed from their nests for the same amount of time as those from the early and late nests (and replaced with artificial eggs) but were then replaced back into their nest of origin.

I defined hatching date as the day the first egg within a

clutch hatched. As soon as all eggs in a clutch had hatched, I captured parent swallows in the nest boxes using a swing-door trap. Females were aged as either second year (SY) or after second year (ASY) based on plumage colour (Hussell 1983). Each bird was weighed with a spring scale (nearest 0.25 g) and the lengths of their ninth primary flight feather, wing chord, and tail were measured with a ruler (nearest 0.5 mm). I estimated body size for all birds captured during 2001 and 2002 using a principal components analysis (PCA), with separate analyses performed for each sex. Lengths of wing, ninth primary, and tail were used as input variables, and the first principal components (PC1) was used as an estimate of size. PC1 explained 73.4% and 70.2% of the variation for females and males, respectively. To estimate body condition of parents, I scaled mass to body size using the residuals calculated from a regression between body size (PC1) and mass, with analyses being performed separately for females ( $F_{[1,89]} = 7.18$ ,  $P < 0.01$ ) and males ( $F_{[1,70]} = 5.58$ ,  $P = 0.02$ ). When nestlings were 6 days old, I weighed them to the nearest 0.25 g with a spring scale. They were again weighed when they were 12 days old, at which time I also measured the length of their ninth primary feather using a ruler (nearest 0.5 mm). As offspring within a nest are not independent observations, I subsequently calculated means for each nest and used these values in statistical analyses. Nests were visited again at 22–24 days following hatching to document any mortality that occurred after 12 days of age.

It has recently been shown that climatic variation can have significant influences on the quality of nestling tree swallows in the vicinity of my study area (Dawson et al. 2005), and so I was also interested in including weather as a covariate in analyses. In each year, mean daily temperature ( $^{\circ}\text{C}$ ) and daily rainfall (mm) from the day the first clutch in the population hatched until the day that the last chick fledged were obtained from an Environment Canada weather station located 15 km north of the study area. Using temperature and rainfall as input variables, I performed a PCA and used PC1 as a measure of daily weather patterns. PC1 explained 74.5% of the variation, with negative values representing favourable conditions (high temperatures and little or no rainfall), while positive values represented more inclement weather conditions.

### Predictions and tests

Prior to testing for the effects of parental quality and timing of breeding on reproductive performance of tree swallows, I first examined whether my manipulation altered the body condition of parents. I used analysis of covariance (ANCOVA) with hatching-date treatment, year, and date of clutch completion to test how condition of parents varied. Date of clutch completion tested for effects related to a bird's chosen timing of breeding, while treatment tested for effects of the manipulation (specifically, lengthening or shortening of the incubation period). Analyses were conducted for both sexes separately, and I also included age (SY, ASY) in the analysis for females.

The underlying assumption of experiments involving timing of breeding is that reproductive success declines among individuals breeding later in the season. I therefore expected that actual hatching date would be a significant predictor of

performance in all models. I further predicted that if variation in success was explained by only the date hypothesis, my manipulation of hatching dates would not be influential in the models because the performance of parents would be determined only by the actual breeding date. Alternatively, if breeding performance of tree swallows was dependent on parental quality, hatching-date treatment would also emerge as a significant predictor in the analyses, with the rationale being that late birds would perform better than controls breeding at the same time, while early birds would have lower success than control birds with the same hatching date (Fig. 1).

Mass of nestlings at 6 and 12 days of age, as well as length of ninth primary at 12 days of age, were each analyzed using an ANCOVA that included hatching-date treatment, year, and female age as categorical variables, and actual hatching date, condition of parents, and weather as covariates. For mass at 6 and 12 days of age, I used the average weather experienced by a nest during the 2 days prior to measurements being taken. For length of ninth primary at 12 days of age, I used average weather between 6 and 11 days of age. My rationale for using these time periods was that body mass of offspring can be quite dynamic and shows a relatively rapid response to variation in weather, primarily because weather can influence the availability of the main food resource of tree swallows, i.e., flying insects (Schew and Ricklefs 1998). Elongation of feathers is more resilient to short-term changes in weather patterns and provisioning, although longer periods of inclement weather should have an impact on the growth of feathers (Schew and Ricklefs 1998). As primary feathers begin growing at around 6 days of age, using weather conditions from the initiation of growth until feathers were measured was appropriate.

To analyze fledging success, I first removed the confounding effect of initial clutch size on number of offspring fledging by calculating the proportion of eggs that produced a fledged offspring. I used an ANCOVA with hatching-date treatment, year, and female age as categorical variables, and actual hatching date and condition of parents as covariates. It was not possible to include the average weather experienced by broods over the entire nestling period because of a strong correlation between weather (from date of hatching until offspring were 18 days old) and hatching date (weather became increasingly mild as the breeding season progressed;  $r = -0.77$ ,  $n = 44$ ,  $P < 0.001$ ). This is in contrast to average weather conditions 2 or 6 days prior to measuring birds that I used in the analyses of mass and length of primaries of chicks, which showed no relationship with hatching date.

Sample sizes differ among analyses because of continual attrition of nests throughout the season resulting from failure and predation. For all analyses, I employed a backwards stepwise approach to sequentially remove interactions and main effects that did not approach significance ( $P > 0.10$ ), and analyses were repeated to obtain the most parsimonious models; however, as hatching-date treatment and hatching date were the primary variables of interest, I always retained these in final models. Data were analyzed using SPSS (Norušis 2000), I considered results significant at the 0.05 level and values are means  $\pm$  1 SE.

## Results

Of 68 nests that were part of this study, 2 were lost when nest boxes were destroyed by livestock and another 7 (10%) pairs abandoned their nests during incubation. While some abandonment may have been due to my manipulation, three of seven abandonments occurred in the control group. Moreover, 8 of 50 (16%) nests not used in this study (but in the same study area) were abandoned, a rate that is not significantly different from my nests ( $G_{[1]} = 0.84$ ,  $P = 0.36$ ). In addition, one nest was lost because of predation during brood-rearing, while 16 pairs of swallows that successfully hatched eggs failed to raise any offspring to fledging. Abandoned and depredated nests, as well as those lost to livestock, were not used in analyses of offspring performance or fledging success.

### Hatching date

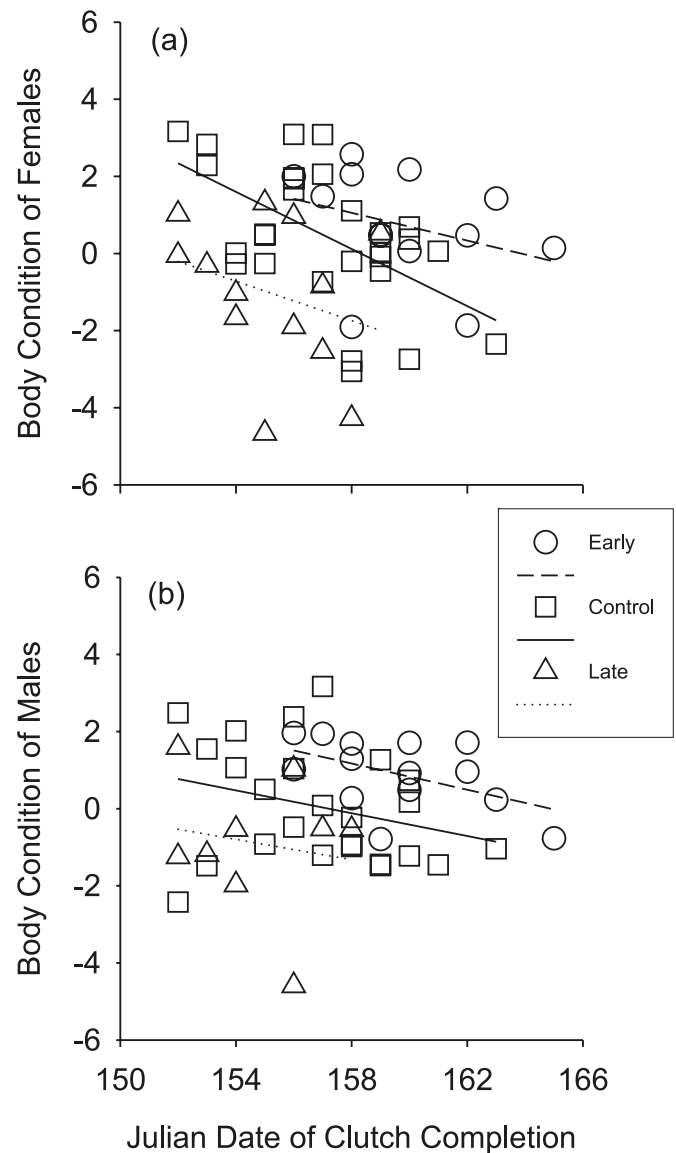
As expected, the analysis testing for post-treatment differences in actual hatching date showed that the date the first egg hatched in clutches differed significantly among treatments ( $F_{[2,56]} = 14.50$ ,  $P < 0.001$ ), and also that hatching dates were earlier in 2001 than in 2002 ( $F_{[1,56]} = 14.42$ ,  $P < 0.001$ ). Post hoc Bonferroni tests revealed that early nests hatched earlier than late nests, while both early and control nests hatched earlier than late nests ( $P < 0.05$ ). Differences between early and control nests approached significance ( $P = 0.06$ ).

### Parental condition

Among female parents, there was some suggestion that older (ASY) birds were in better body condition than younger (SY) ones ( $F_{[1,49]} = 3.22$ ,  $P = 0.08$ ). This analysis also showed that condition of females declined significantly with later dates of clutch completion ( $F_{[1,49]} = 13.32$ ,  $P < 0.001$ ) and was significantly affected by hatching-date treatment ( $F_{[2,50]} = 8.52$ ,  $P < 0.01$ ; Fig. 2). Post hoc tests (Bonferroni) showed that both control and early females were in significantly better condition than females in the late group ( $P < 0.01$ ). Similar results were found for males, where body condition declined significantly with later dates of clutch completion ( $F_{[1,44]} = 4.14$ ,  $P = 0.048$ ) and was significantly affected by treatment ( $F_{[2,44]} = 6.80$ ,  $P < 0.01$ ; Fig. 2). Post hoc tests showed that early males were in significantly better condition than both control and late males (both  $P$  values  $< 0.03$ ), but that there were no differences between control and late males ( $P > 0.05$ ).

Further analyses were performed to investigate the nature of the seasonal changes in body condition of parents, specifically whether these patterns were the consequence of lengthening or shortening the incubation period, and hence representative of biases induced by the experimental manipulation (see Wardrop and Ydenberg 2003). Several lines of evidence, however, suggest that my results were due to early and late birds simply being captured earlier or later, respectively, in the season and not because birds that were forced to incubate longer did so at a cost to their body condition. When data on condition were reanalyzed with actual hatching date instead of date of clutch completion as a covariate, condition declined significantly with later dates of hatching for both sexes (females:  $F_{[1,49]} = 16.57$ ,  $P < 0.001$ ; males:

**Fig. 2.** Body condition of adult (a) female and (b) male tree swallows (*Tachycineta bicolor*) in relation to Julian date of clutch completion for control nests and those where hatching date was experimentally advanced (early) or delayed (late) by 4 days. See Materials and methods for details on calculation of body condition.



$F_{[1,44]} = 4.40$ ,  $P = 0.04$ ), but treatment was no longer a significant predictor of condition (females:  $F_{[2,49]} = 0.60$ ,  $P = 0.56$ ; males:  $F_{[2,44]} = 1.95$ ,  $P = 0.15$ ). These results show that it is hatching date, and not length of the incubation period (and hence treatment), that is driving variation in adult condition. Moreover, when I used partial correlation analysis to control for date of hatching, there was no relationship between the length of the incubation period (in days) and condition of female parents (partial  $r = -0.08$ ,  $df = 51$ ,  $P = 0.56$ ). Second, male tree swallows do not incubate (Robertson et al. 1992) and so decreasing or increasing the length of the incubation period cannot directly account for the results for males. Nonetheless, even if declines in condition are driven only by later hatching dates and not by changes in incubation period, the results of my experiment may still have been affected, and so I averaged the condition index of

both parents for each nest and used this as a covariate in all subsequent analyses.

### Offspring performance

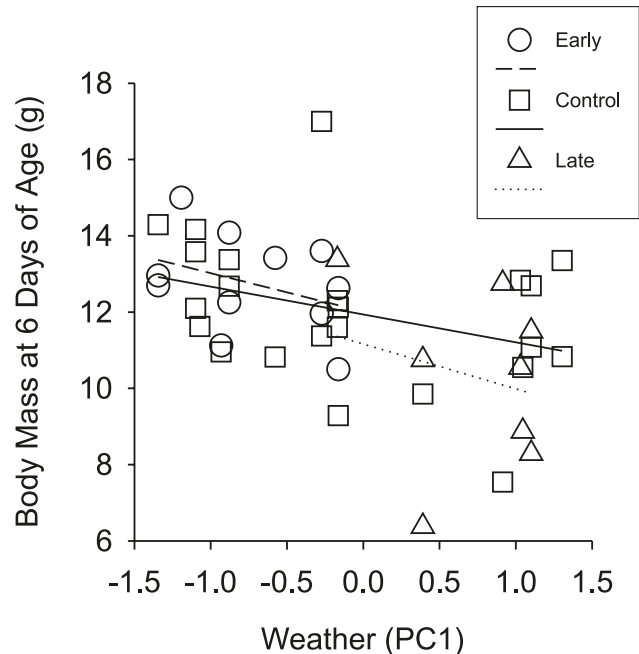
Mass of nestlings at 6 and 12 days of age, as well as length of ninth primary at 12 days of age, were each analyzed using ANCOVA models that included hatching-date treatment, female age, and year as categorical variables, and actual hatching date, condition of parents, and weather as covariates. There was no effect of hatching-date treatment ( $F_{[2,37]} = 1.17$ ,  $P = 0.32$ ) or hatching date ( $F_{[1,37]} = 0.61$ ,  $P = 0.44$ ) on mass of nestlings at 6 days of age, but mass of chicks declined significantly as the weather they were exposed to for the 2 days prior became more inclement ( $F_{[1,37]} = 4.55$ ,  $P = 0.04$ ; Fig. 3). At 12 days of age, there was no effect of treatment ( $F_{[2,30]} = 0.55$ ,  $P = 0.59$ ) or hatching date ( $F_{[1,30]} = 0.12$ ,  $P = 0.73$ ) on mass of chicks, but there was again a significant effect of weather during the 2 days prior to measurement ( $F_{[1,30]} = 8.95$ ,  $P < 0.01$ ). However, the interaction between hatching-date treatment and weather was also significant ( $F_{[1,30]} = 4.42$ ,  $P = 0.02$ ), suggesting that the relationships between weather and offspring mass varied according to treatment. To further investigate this issue, I analysed relationships between weather and mass at 12 days of age separately for each treatment using correlation analyses. The relationship between mass of offspring and weather was significant both in control nests ( $r = -0.44$ ,  $n = 22$ ,  $P = 0.04$ ) and late nests ( $r = -0.82$ ,  $n = 6$ ,  $P = 0.047$ ); however, there was no relationship between weather and mass in early nests ( $r = 0.25$ ,  $n = 9$ ,  $P = 0.52$ ). There was no effect of either treatment ( $F_{[2,32]} = 0.07$ ,  $P = 0.93$ ) or hatching date ( $F_{[1,32]} = 0.76$ ,  $P = 0.39$ ) on length of ninth primaries of chicks at age 12 days, but there was some suggestion that inclement weather during the previous 6 days was associated with shorter primaries ( $F_{[1,32]} = 3.25$ ,  $P = 0.08$ ; Fig. 4). Age of females and condition of parents were not significant predictors in any of the above analyses and were subsequently removed from models.

There was no significant effect of hatching-date treatment on proportion of offspring fledging ( $F_{[2,53]} = 0.50$ ,  $P = 0.61$ ); however, more young were fledged in 2001 than in 2002 ( $F_{[1,53]} = 8.12$ ,  $P < 0.01$ ), and number fledged decreased significantly as hatching dates became later in the season ( $F_{[1,53]} = 5.07$ ,  $P = 0.03$ ; Fig. 5).

### Discussion

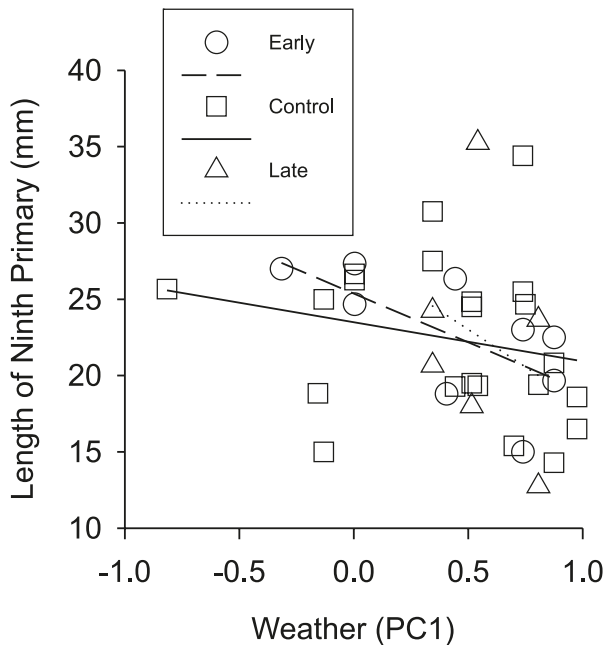
Timing of breeding is an important factor determining reproductive success in many species of birds. Decreased success among late breeders may be the result of lower quality parents breeding later in the season, or because of systematic environmental changes that occur during the season, making conditions less favourable for late-breeding birds. It has even been suggested that optimal breeding time varies among individual pairs so that either advancing or delaying breeding will result in lower reproductive success (individual optimization hypothesis; Daan et al. 1990; Aparicio 1998). In my study, I found some support for the date hypothesis, as those birds breeding earlier in the season were more successful at fledging offspring (Fig. 5). A previous manipulative study investigating timing of breeding in

**Fig. 3.** Body mass of nestling tree swallows (*Tachycineta bicolor*) at 6 days of age in relation to weather conditions during the 2 days prior to measurement. Data are for nests where hatching date was experimentally advanced (early) or delayed (late) and for control nests. Weather is a composite measure derived from a principal components (PC) analysis (see Materials and methods). Negative PC1 values represent favourable conditions (high temperatures and little or no rainfall), whereas positive values represent more inclement weather conditions.



tree swallows (Wardrop and Ydenberg 2003) did not directly examine fledging success, as brood size was adjusted to 6 young in all nests. In great tits (*Parus major* L., 1758), however, Verhulst et al. (1995) found that while parental quality was a predictor of fledging success, recruitment of offspring appeared to be related to timing. Similarly, Svensson (1997) found that delayed pairs of blue tits (*Cyanistes caeruleus* (L., 1758)) had a lower proportion of their young recruit to the breeding population, possibly because late young were of low quality. Norris (1993) also found that postfledging survival of blue tits was related to timing and he suggested that the mechanism may be declining food supplies for later breeding birds, which could affect dispersal and subsequent settlement. While postfledging dispersal cannot account for my results, it seems likely that reduced fledging success of late breeders was linked with food supply so that even when in the nest late birds are faced with significantly fewer resources in the environment. Such effects would likely also be exasperated after fledging because juvenile swallows begin to migrate soon after leaving the nest and so would need to acquire experience and increase their body condition immediately upon fledging. Unfortunately, philopatry of tree swallows to natal areas is low (Robertson et al. 1992) and so I was not able to examine recruitment in relation to timing of breeding in the present study. Ardia et al. (2006) have recently shown that female tree swallows breeding early in the season invest more in egg yolk, and so differential allocation of resources to eggs

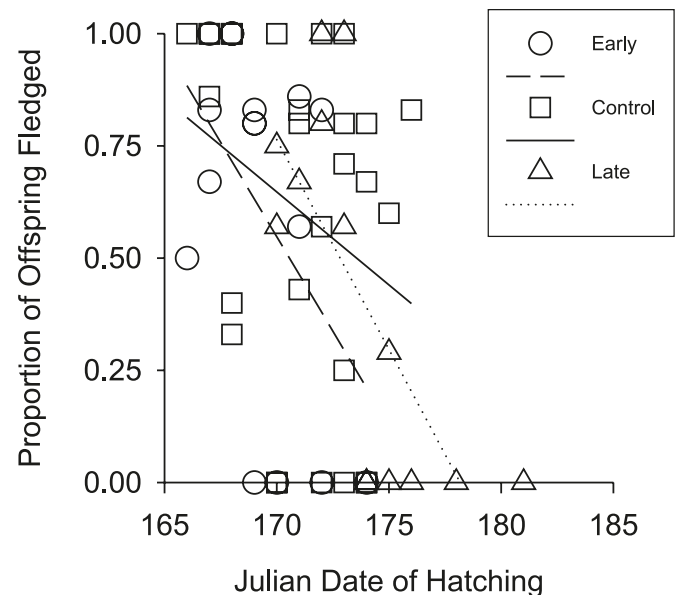
**Fig. 4.** Length of ninth primary flight feather of nestling tree swallows (*Tachycineta bicolor*) at 12 days of age in relation to weather conditions from ages 6 to 11 days. Data are for nests where hatching date was experimentally advanced (early) or delayed (late) and for control nests. Weather is a composite measure derived from a principal components (PC) analysis (see Materials and methods). Negative PC1 values represent favourable conditions (high temperatures and little or no rainfall), whereas positive values represent more inclement weather conditions.



may also partly explain higher fledging success among early breeders.

It is well-recognized that manipulative experiments which alter timing of breeding have the potential to unintentionally introduce bias (Norris 1993; Verhulst and Nilsson 2008). Removing first clutches to induce later breeding forces females to produce an entire replacement clutch of eggs, while clutch-swap protocols vary the period of time that parents must incubate. In general, however, most studies have suggested that both of these methods have little effect on parents (e.g., Verhulst et al. 1995; Sanz 1999; Christians et al. 2001). In contrast, Wardrop and Ydenberg (2003) found that condition of female tree swallows was significantly affected by their clutch-swapping protocol, and I showed that some variation in body condition of parents was explained by my swapping experiment (Fig. 2). While I believe that changes in body condition of parents was related to timing of capture during the breeding season rather than variation in incubation periods per se (see Results), it is clear that my experimental groups differed with respect to condition, which may have influenced my results. However, inclusion of body condition as a potential covariate did not significantly improve the models for any variable analyzed and so experimental bias seems unlikely in my study. Moreover, Winkler and Allen (1996) found no consistent effect of multiple measures of condition on timing of breeding and hence seasonal decline in clutch size of tree swallows, and concluded that body condition is a weak and inconsistent factor determining reproductive output of female tree swallows.

**Fig. 5.** Proportion of offspring fledging in relation to Julian hatching date of tree swallows (*Tachycineta bicolor*). Data are for nests where hatching date was experimentally advanced (early) or delayed (late) and for control nests. Proportion fledged was calculated as number of young fledged divided by initial clutch size.



An implicit assumption of studies investigating mechanisms related to timing of breeding is that performance actually declines among birds naturally breeding later in the season (Fig. 1), and there is abundant evidence that this is the case for many species of birds (e.g., Norris 1993; Spear and Nur 1994; Verhulst et al. 1995; Aparicio 1998). Wardrop and Ydenberg (2003) found that the date hypothesis explained mass of nestling tree swallows early in the season, whereas parental quality better explained the variation in mass among later breeding pairs. In my present study of tree swallows, body mass and length of ninth primary feathers were unrelated to both hatching date and hatching-date treatment, suggesting that neither timing nor parental quality induced significant variation in these characteristics of offspring. Instead, I showed that birds were significantly lighter and tended to have shorter feathers when they had been exposed to inclement weather (Figs. 3, 4), although mass at age 12 days appeared to not be affected by weather in nests where parents had been manipulated to breed earlier than anticipated. Effects of weather were probably the consequence of reduced provisioning by parents during cold and rainy weather (e.g., Nooner et al. 2005). In addition, recent experimental work on tree swallows near my study area has also shown that higher nest temperatures can significantly enhance size and growth of nestlings (Dawson et al. 2005). Both the present study and previous results (Dawson et al. 2005; Nooner et al. 2005) suggest that environmental influences are important determinants of offspring quality in tree swallows breeding in temperate landscapes.

Weather conditions became less inclement in my study area as the breeding season progressed. Therefore, the thermal environment of the nest would also have become more favourable as the season progressed, potentially providing benefits for nestlings (Dawson et al. 2005). Nonetheless, de-

spite such increases in temperature, tree swallows in my study area appear to be extremely susceptible to short periods of inclement weather. In some years it is possible for temperatures to approach the freezing point and there have been brief snow storms in the vicinity of my study area during early July (personal observation). Inclement weather can affect nestlings directly by increasing thermoregulatory costs and indirectly by hampering the ability of parents to procure food (Dawson and Bortolotti 2000). In both cases, these somewhat random events can cause slow growth rates and high mortality of offspring. For example, considering nests that hatched at least one egg over the 2 years of my study, 34% of nests failed ( $n = 97$ ) and over 55% of all offspring ( $n = 463$ ) in my study area died before fledging, presumably from effects related to inclement weather (unpublished data). This is in sharp contrast to other studies of tree swallows, where mortality rates of nestlings are very much lower. Whittingham and Dunn (2001) reported that only 5% of 281 nestlings died, while Wardrop and Ydenberg (2003) lost just over 17% of 46 nests during brood-rearing in their study of tree swallows. Robertson et al. (1992) reported that about 20% of nests fail to produce young. It seems that because of the importance of unpredictable weather events in my study area, any relationship between timing of breeding or parental quality and offspring performance have become uncoupled, at least during the years when this investigation occurred.

Declines in reproductive success among late-breeding birds have received considerable study over the past decade. Although manipulative studies have supported either the quality or date hypotheses and, in some cases, both (e.g., Brinkhof 1997; Wardrop and Ydenberg 2003), there appears to be more support for hypotheses related to timing (see Nilsson 1999, 2000; Arnold et al. 2004). Winkler and Allen (1996) suggested that reduced reproductive effort, and therefore success, among late-breeding tree swallows was a strategic adjustment by females in response to seasonal changes in the survival prospects of young hatched at different times during the breeding season. They reasoned that late-breeding parents would accrue more benefit by investing less in these offspring with reduced recruitment probabilities and instead save energy and other resources for self-maintenance that would enhance their own prospects of survival to the next breeding episode. Nonetheless, to fully understand the fitness consequences of timing of breeding, it will be necessary to not only determine why late-breeding birds perform less well, but also to elucidate what constrains them from breeding earlier in the first place.

## Acknowledgements

I wish to thank P.-P. Bitton and K. Maitland for help with fieldwork, and G. Sanders and the late R. Dykes for allowing me to access their properties. R. Ydenberg and anonymous reviewers provided critical comments that improved an earlier draft of the manuscript. Funding for this research was provided by the Natural Sciences and Engineering Research Council of Canada, Canada Foundation for Innovation, British Columbia Knowledge Development Fund, and University of Northern British Columbia through grants to R.D.D.

## References

- Aparicio, J.M. 1998. Individual optimization may explain differences in breeding time in the European kestrel *Falco tinnunculus*. *J. Avian Biol.* **29**: 121–128. doi:10.2307/3677189.
- Ardia, D.R., Wasson, M.F., and Winkler, D.W. 2006. Individual quality and food availability determine yolk and egg mass and egg composition in tree swallows *Tachycineta bicolor*. *J. Avian Biol.* **37**: 252–259. doi:10.1111/j.2006.0908-8857.03624.x.
- Arnold, J.M., Hatch, J.J., and Nisbet, I.C.T. 2004. Seasonal declines in reproductive success of the common tern *Sterna hirundo*: timing or parental quality? *J. Avian Biol.* **35**: 33–45. doi:10.1111/j.0908-8857.2004.03059.x.
- Brinkhof, M.W.G. 1997. Seasonal decline in body size of coot chicks. *J. Avian Biol.* **28**: 117–131. doi:10.2307/3677305.
- Bryant, D.M. 1975. Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. *Ibis*, **117**: 180–214. doi:10.1111/j.1474-919X.1975.tb04206.x.
- Christians, J.K., Evanson, M., and Aiken, J.J. 2001. Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. *J. Anim. Ecol.* **70**: 1080–1087. doi:10.1046/j.0021-8790.2001.00566.x.
- Clutton-Brock, T.H. 1988. *Reproductive success*. University of Chicago Press, Chicago.
- Cushman, J.H., Boggs, C.L., Weiss, S.B., Murphy, D.D., Harvey, A.W., and Ehrlich, P.R. 1994. Estimating female reproductive success of a threatened butterfly: influence of emergence time and host plant phenology. *Oecologia (Berl.)*, **99**: 194–200. doi:10.1007/BF00317101.
- Daan, S., Dijkstra, C., and Tinbergen, J.M. 1990. Family planning in the kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. *Behaviour*, **114**: 83–116. doi:10.1163/156853990X00068.
- Dawson, R.D., and Bortolotti, G.R. 2000. Reproductive success of American kestrels: the role of prey abundance and weather. *Condor*, **102**: 814–822. doi:10.1650/0010-5422(2000)102[0814:RSOAKT]2.0.CO;2.
- Dawson, R.D., Lawrie, C.C., and O'Brien, E.L. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia (Berl.)*, **144**: 499–507. doi:10.1007/s00442-005-0075-7.
- Heaney, V., and Monaghan, P. 1996. Optimal allocation of effort between reproductive phases: the trade-off between incubation costs and subsequent brood rearing capacity. *Proc. R. Soc. Lond. B Biol. Sci.* **263**: 1719–1724. doi:10.1098/rspb.1996.0251.
- Hussell, D.J.T. 1983. Age and plumage color in female tree swallows. *J. Field Ornithol.* **54**: 312–318.
- Nilsson, J.-Å. 1999. Fitness consequences of timing of reproduction. *Birdlife South Africa*, **1999**: 234–247.
- Nilsson, J.-Å. 2000. Time-dependent reproductive decisions in the blue tit. *Oikos*, **88**: 351–361. doi:10.1034/j.1600-0706.2000.880214.x.
- Nooker, J.K., Dunn, P.O., and Whittingham, L.A. 2005. Effects of food abundance, weather, and female condition on reproduction in tree swallows (*Tachycineta bicolor*). *Auk*, **122**: 1225–1238. doi:10.1642/0004-8038(2005)122[1225:EOFAWA]2.0.CO;2.
- Norris, K. 1993. Seasonal variation in the reproductive success of blue tits: an experimental study. *J. Anim. Ecol.* **62**: 287–294. doi:10.2307/5360.
- Norušis, M.J. 2000. *SPSS: advanced statistics user's guide*. SPSS Inc., Chicago.
- Price, T., Kirkpatrick, M., and Arnold, S.J. 1988. Directional selection and the evolution of breeding date in birds. *Science*

- (Washington, D.C.), **240**: 798–799. doi:10.1126/science.3363360. PMID:3363360.
- Reid, J.M., Monaghan, P., and Ruxton, G.D. 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proc. R. Soc. Lond. B Biol. Sci.* **267**: 37–41. doi:10.1098/rspb.2000.0963.
- Robertson, R.J., Stutchbury, B.J., and Cohen, R.R. 1992. Tree swallow. *In* The birds of North America. No. 11. *Edited by* A. Poole, P. Stettenheim, and F. Gill. The Academy of Natural Sciences, Philadelphia, Pa.; The American Ornithologists' Union, Washington, D.C. pp. 1–28.
- Sanz, J.J. 1999. Seasonal variation in reproductive success and post-nuptial moult of blue tits in southern Europe: an experimental study. *Oecologia (Berl.)*, **121**: 377–382. doi:10.1007/s004420050942.
- Schew, W.A., and Ricklefs, R.E. 1998. Developmental plasticity. *In* Avian growth and development. *Edited by* J.M. Starck and R.E. Ricklefs. Oxford University Press, Oxford. pp. 288–304.
- Spear, L., and Nur, N. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. *J. Anim. Ecol.* **63**: 283–298. doi:10.2307/5547.
- Svensson, E. 1997. Natural selection on avian breeding time: causality, fecundity-dependent, and fecundity-independent selection. *Evolution*, **51**: 1276–1283. doi:10.2307/2411056.
- Verhulst, S., and Nilsson, J.A. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philos. Trans. R. Soc. B Biol. Sci.* **363**: 399–410. doi:10.1098/rstb.2007.2146.
- Verhulst, S., van Balen, J.H., and Tinbergen, J.M. 1995. Seasonal decline in reproductive success of the great tit: variation in time or quality? *Ecology*, **76**: 2392–2403. doi:10.2307/2265815.
- Wardrop, S.L., and Ydenberg, R.C. 2003. Date and parental quality effects in the seasonal decline in reproductive performance of the tree swallow *Tachycineta bicolor*: interpreting results in light of potential experimental bias. *Ibis*, **145**: 439–447. doi:10.1046/j.1474-919X.2003.00184.x.
- Whittingham, L.A., and Dunn, P.O. 2001. Survival of extrapair and within-pair young in tree swallows. *Behav. Ecol.* **12**: 496–500. doi:10.1093/beheco/12.4.496.
- Winkler, D.W., and Allen, P.E. 1996. The seasonal decline in tree swallow clutch size: physiological constraint or strategic adjustment? *Ecology*, **77**: 922–932. doi:10.2307/2265512.