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A test of the mismatch hypothesis: How is timing of reproduction related to food abundance in an aerial insectivore?

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Abstract. In seasonal environments, vertebrates are generally thought to time their reproduction so offspring are raised during the peak of food abundance. The mismatch hypothesis predicts that reproductive success is maximized when animals synchronize their reproduction with the food supply. Understanding the mechanisms influencing the timing of reproduction has taken on new urgency as climate change is altering environmental conditions during reproduction, and there is concern that species will not be able to synchronize their reproduction with changing food supplies. Using data from five sites over 24 years (37 site-years), we tested the assumptions of the mismatch hypothesis in the Tree Swallow (*Tachycineta bicolor*), a widespread aerial insectivore, whose timing of egg-laying has shifted earlier by nine days since the 1950s. Contrary to the mismatch hypothesis, the start of egg-laying was strongly related to food abundance (flying insect biomass) during the laying period and not to timing of the seasonal peak in food supply. In fact, food abundance generally continued to increase throughout the breeding season, and there was no evidence of selection based on the mistiming of laying with the seasonal peak of food abundance. In contrast, there was selection for laying earlier, because birds that lay earlier generally have larger clutches and fledge more young. Overall, initial reproductive decisions in this insectivore appear to be based on the food supply during egg formation and not the nestling period. Thus, the mismatch hypothesis may not apply in environments with relatively constant or abundant food throughout the breeding season. Although climate change is often associated with earlier reproduction, our results caution that it is not necessarily driven by selection for synchronized reproduction.

Key words: aerial insectivores; birds; climate change; food abundance; insects; life history; mismatch hypothesis; predictability; *Tachycineta bicolor*; Tree Swallow.

Most birds have a restricted breeding season, which is so timed that the young are being raised when their food is most plentiful. This season may vary somewhat from year to year.

—David Lack (1954:66)

INTRODUCTION

In seasonal environments the timing of reproduction poses a fundamental challenge to iteroparous animals. Selection is thought to generally favor earlier reproduction, because it increases the number of surviving offspring, but on the other hand, earlier reproduction may decrease adult survival if food and weather are less predictable (Perrins 1970, Price et al. 1988, Goutis and Winkler 1992). Pioneering studies of European tits (*Parus* spp.) by Lack (1954) and Perrins (1970) showed a correlation between the timing of peaks in energetic

demands of nestlings and the abundance of their food (caterpillars). This led to the widespread belief that birds time their laying so that hatching coincides with seasonal peaks in food supply before it starts to decline later in the season (Lack 1954, Perrins 1970, Daan et al. 1989). Thus, timing of laying is often viewed as a trade-off between the advantages of hatching early for nestlings and the disadvantages to females who may risk their own survival by laying early when food is less abundant (Drent 2006).

Understanding the mechanisms influencing the timing of reproduction has taken on new urgency as climate change is altering environmental conditions during reproduction, and several studies suggest that species are not responding sufficiently to environmental changes by shifting their breeding phenology (Visser and Both 2005). In particular, some species have not advanced their breeding phenology at the same rate as changes in temperature or food supply, and this temporal mismatch has led to increased selection for earlier reproduction (Visser et al. 1998, Nielsen and Møller 2006, Reed et al. 2009, van der Jeugd et al. 2009; reviewed by Both [2010]

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and Dunn and Winkler [2010]). Comparative evidence also suggests that populations of migratory birds in Europe are more likely to be declining if they have not adjusted their timing of arrival on the breeding grounds in response to climate warming (Møller et al. 2008).

This temporal mismatch hypothesis was first proposed to explain annual variation in cod recruitment based on how closely fish larvae matched the peaks in zooplankton (Cushing 1990), but it has been applied to a wide variety of predators and prey reproducing in seasonal environments (reviewed by Durant et al. [2007]). The hypothesis assumes that, first, the food supply for predators is seasonal and abundant only for a portion of the reproductive season, limiting the optimal period for reproduction. For example, the food supply (aerial insects) of Barn Swallows (*Hirundo rustica*) declines in late summer limiting the survival of young from second broods (Grüebler and Naef-Daenzer 2008). Note that it is possible for the length of the reproductive season to be limited for other reasons besides the food supply, such as time constraints on offspring development (Varpe et al. 2007), but this would not necessarily involve synchrony with the peak of food supply. Second, the mismatch hypothesis assumes that selection favors individuals that time their reproduction so the peak food demands of their offspring match the seasonal peak of prey abundance. As a consequence, reproductive success will be greater the closer the timing of reproduction matches the peak of food abundance. In some species it is also assumed that temperature and food supply during laying are simply cues to synchronize reproduction with the food supply later in the season, rather than being energetic constraints on producing eggs (Daan et al. 1989). In this case, there is a third assumption that environmental cues during laying are good predictors of the timing of food supply later in the season when offspring energetic demands are greatest. Testing these three assumptions is important, because it has been suggested that the size of mismatches can be used to judge the impacts of climate change on species (Visser and Both 2005). To date, however, there are few long-term data available to study how shifts in predator phenology are coupled to changes in their food supply (reviewed by Visser and Both [2005]).

In this study, we tested the assumptions of the mismatch hypothesis in Tree Swallows (*Tachycineta bicolor*), which feed exclusively on aerial insects during breeding (see Plate 1). We also determined whether timing of laying corresponds more closely with environmental conditions (temperature and food abundance) during egg formation (Perrins 1970) or the nestling period (Lack 1954). Although it has been suggested that the food supply of aerial insectivores is relatively unpredictable (e.g., Bryant 1975, Cucco and Malacarne 1996), previous studies have been relatively short term, and they have not directly tested the other assumptions of the mismatch hypothesis. Our study spanned five locations across Canada and the northern United States

over a period of 24 years (37 site-years total). Our insect sampling at these sites allowed us to examine variation in food supply under a wide variety of environmental conditions and, thus, we could also test whether the food supply for nestlings was predictable based on conditions at the beginning of the breeding season. In contrast to studies of European tits, we show that the assumptions of the mismatch hypothesis generally do not hold in this aerial insectivore. In particular, there is no strong peak in food abundance as it generally increases throughout the season, and as a consequence, there is no significant selection due to temporal mismatches with the food supply for nestlings.

METHODS

Tree Swallows are a common and widespread breeding species in the northern United States and Canada. They use secondary cavities in trees as nest sites, although they readily accept nest boxes as alternatives to natural cavities. Swallows typically arrive on the breeding grounds in late March to mid-April, presumably as a consequence of competition for nest sites, as laying usually starts in May, at least several weeks after most birds have arrived (Stutchbury and Robertson 1987). The date of clutch initiation (laying date) averages 20 May (± 1.1 d, $n = 37$ site-years, range of yearly means = 14 May to 15 June). Tree Swallows usually produce a single brood each season, and clutch size ranges from 3 to 8 eggs, although clutches of 5 and 6 eggs are most common (Robertson et al. 1992). Females incubate the clutch alone, but both sexes provide food to the nestlings, which typically fledge at 18–22 days.

We studied Tree Swallows nesting in boxes at five locations: Beaverhill Lake, Tofield, Alberta, Canada (53°23' N, 112°31' W; 1986–1988) (Dunn and Hannon 1992); Cornell University Ponds, Ithaca, New York, USA (42°29' N, 76°28' W; 1989–2002) (Winkler and Allen 1996); Queen's University Biological Station, Chaffey's Locks, Ontario, Canada (44°34' N, 76°20' W; 1989–1990) (Robertson and Rendell 1990, Dunn and Robertson 1992); University of Wisconsin–Milwaukee Field Station, Saukville, Wisconsin, USA (43°23' N, 88°01' W; 1997–2009) (Whittingham and Dunn 2000); and Yellowknife, Northwest Territories, Canada (62°27' N, 114°19' W; 1988–1989). From these sites we collected data on timing of laying and daily air temperature for a total of 37 site-years. Mean daily air temperature was estimated from weather stations at the New York, Wisconsin, and Ontario sites or from Environment Canada weather stations at airports near Beaverhill Lake (Edmonton International, 70 km away) or Yellowknife (9 km).

To estimate food abundance, flying insects were sampled at all five sites for a total of 26 site-years (Dunn and Hannon 1992, Dunn and Robertson 1992, Ardia et al. 2006). We collected insects with tow nets (Hussell and Quinney 1985) and suction traps (Taylor and Palmer 1972, McCarty and Winkler 1999). Tow nets positioned 2

m above ground were used in Alberta (1986–1988), Ontario (1990), Wisconsin (1997–1999), and the Northwest Territories (1988). Suction traps included a 12-m Rothamsted sampler (Macaulay et al. 1972), which was used in Ithaca during 1989 through 2002, and a smaller 1.5-m suction trap, which was used in Wisconsin during 2000–2003 and in 2008 and 2009. Each day traps were operated for at least 80% of daylight hours, and at each location, samples were collected an average of 103 days each season from before egg-laying (median start 1 May) until over 90% of birds had fledged (median finish 1 July; excluding two site-years with sampling only during the laying period). Biomass of insects was estimated from length-mass relationships calculated for different taxa dried to constant mass (Dunn and Hannon 1992). These insect traps collect all of the taxa eaten by swallows (Hussell and Quinney 1985, Dunn and Hannon 1992), and they provide estimates of food abundance that are correlated with timing of laying and reproductive performance (Hussell and Quinney 1985, Nooker et al. 2005).

We used the 25th percentile of clutch initiation dates (laying dates) as an index of the beginning of laying for each population and year. This avoids extremely early nests and represents the beginning of laying better than the mean laying date, although for comparative purposes we also use the mean laying date in some analyses. Food abundance during the beginning of egg-laying was estimated for each population and year using the average insect biomass (log-transformed) during the five days prior to the 25th percentile of laying dates. We used this 5-d period because the estimated time for rapid yolk synthesis is five to six days in Tree Swallows (Ardia et al. 2006), and, thus, five days allowed us to capture the effects of food on laying throughout the period of rapid yolk accumulation and the formation of the remainder of the egg.

To test the third assumption, we examined insect abundance during the laying period to determine if it was correlated with the timing and abundance of insects during the nestling period, and thus, a potential predictor of food availability later in the season, as assumed by Lack's hypothesis. For this analysis, laying period was defined as the period from the 25th percentile of laying dates to the 75th percentile of laying dates. The nestling period was defined as the period from the 25th percentile of hatch dates to 15 days after the 75th percentile of hatch dates. We used 15 days after hatch to define the end of the nestling period, as fledging can occur after this age and nestlings have reached their asymptotic body mass (Winkler and Adler 1996). We also analyzed insect abundance using the 10th to 90th percentiles of laying and hatching dates, and the results were qualitatively similar (see *Results: Assumption 3*).

Statistical analysis

We used mixed models in JMP version 5 (SAS Institute 2003) to test the assumptions of the mismatch

hypothesis that: (1) the food supply declines later in the season, limiting the optimal period of laying, (2) selection favors individuals that time their laying to match the peak of food abundance for their nestlings later in the season, and (3) the date of peak of food supply can be predicted from conditions at the start of the breeding season (insect biomass averaged over 5 d before the 25th percentile of laying dates). To examine selection, we calculated linear and quadratic selection gradients on standardized laying date following the regression approach of Lande and Arnold (1983). Linear selection gradients were used to test whether selection on reproductive success favored birds that laid earlier relative to the peak of food abundance (directional selection), and quadratic selection gradients were used to test whether selection favored birds that laid closer to the peak of food abundance (i.e., stabilizing selection). We used relative fledging success (individual fledging success divided by mean success for each year and location) as our measure of relative annual fitness because natal recruitment rates are low (<5%) in our populations. For these analyses, laying dates were standardized for each year and site by subtracting each observation from the mean laying date and dividing by the standard deviation. Selection gradients were estimated as the slope of the regression of relative fledging success on standardized laying date. To test whether selection was stronger when there was a greater mismatch between the timing of laying and the food supply, selection gradients for each year and site were regressed on the difference in days between mean laying date and the peak of insect biomass for each site-year (see also van Noordwijk et al. 1995).

RESULTS

The average start of egg-laying (25th percentile of laying dates) varied from 9 to 25 May in all populations (mean \pm SE = 16 May \pm 1.1 d, n = 37 site-years) except Yellowknife, where the 25th percentile of laying was 5 and 10 June in 1989 and 1988, respectively. Estimates of daily insect biomass during the pre-laying period (5 d before the 25th percentile of laying dates) were greater for the suction trap (41 ± 8.3 mg/d) than the tow nets (16 ± 6.2 mg/d; t test on log-transformed data; $t_{119} = 3.56$, $P < 0.001$), so the type of insect sampler was included in all analyses that used insect data from different sites and years.

The beginning of egg-laying in each population (25th percentile of laying dates) was generally earlier when air temperatures in early May were warmer (Table 1). The start of egg-laying was also earlier when pre-laying insect biomass was greater (log-transformed biomass five days before the 25th percentile of laying dates; $F_{1,19} = 6.9$, $P = 0.016$) in a model that also included study site ($F_{4,19} = 10.6$, $P < 0.001$) and type of insect sampler ($F_{1,19} < 0.1$, $P = 0.82$; $R^2 = 0.76$, $n = 26$ site-years; Table 1).

TABLE 1. Regression analyses of the 25th percentile of egg-laying dates (n = site-years) by Tree Swallows (*Tachycineta bicolor*) in relation to mean air temperature and insect biomass (log-transformed) in five locations across Canada and the northern United States.

Predictors	R^2	b	P	n
Temperature				
1–5 May	0.79	–0.74	<0.001	37
6–10 May	0.76	–0.69	0.003	37
11–15 May	0.76	–0.64	0.003	37
5 d <25th percentile of laying dates†	0.74	–0.46	0.01	37
Insect biomass				
1–5 May	0.32	–3.17	0.029	16‡
6–10 May	0.46	–2.45	0.051	23
11–15 May	0.38	–1.57	0.17	25
5 d <25th percentile of laying dates	0.76	–5.65	0.016	26
Date of maximum biomass	0.70	0.07	0.26	26

Notes: Initial regression models included study site and, for insect biomass, the type of insect sampler. R^2 is for the overall model, and P values are from partial F tests for temperature or insect biomass.

† Refers to the daily temperatures or insect biomass averaged over 5 days before the 25th percentile of laying dates.

‡ Only includes site-years with at least three days of sampling during this period; i.e., New York (NY), Ontario (ON), and 2002, 2008, and 2009 in Wisconsin (WI).

Assumption 1: Seasonal declines in food supply limit the time for reproduction

Contrary to the first assumption of the mismatch hypothesis, daily estimates of food abundance generally increased (Fig. 1), rather than decreased, during the nestling period (25th percentile of hatch dates to 15 days after the 75th percentile of hatch; date effect: $F_{1,484} = 12.1$, $P < 0.001$) in a model that also included type of insect sampler, year, and site as random effects (overall $R^2 = 0.53$, $F_{22,484} = 26.4$, $P < 0.001$). There was also a significant increase in insect biomass (log-transformed) across the entire season at our long-term sites in New York ($b = 0.03 \pm 0.003$; $r^2 = 0.12$, $n = 686$ d, $F_{1,684} = 89.5$, $P < 0.001$) and Wisconsin ($b = 0.02 \pm 0.004$; $r^2 = 0.05$, $n = 477$ d, $F_{1,475} = 23.7$, $P < 0.001$). Overall, food abundance was greater during the nestling period (44.2 ± 5.5 mg/d) than during the 5 d before the start of laying (31.8 ± 7.7 mg/d; paired $t_{23} = 2.5$, $P = 0.017$).

Although there was a seasonal increase in food abundance, the variation explained by calendar date was low and the increase was not consistent over the entire season (Fig. 1; early May to late June–early July). Using linear regression, insect biomass increased significantly in 12 of 24 site-years (only site-years with >40 days of sampling), remained relatively constant in nine site-years and declined in one site-year (Alberta 1987; Appendix A: Table A1). Closer inspection of the trends with splines revealed that some years started with high insect biomass and then dipped before increasing later in the season (e.g., NY 2001, WI 2001; see Appendix B: Fig. B1, 2). Thus, food abundance generally increased during the breeding season, but there was only a consistent linear increase in 50% (12/24) of site-years.

Laying date was not associated with the peak of food abundance

The start of laying was not associated significantly with the seasonal peak of food abundance. The 25th percentile of laying dates was not related to the date of maximum insect biomass during the breeding season ($b = 0.03 \pm 0.06$; Table 1) in a model that included study site ($F_{4,19} = 7.4$, $P < 0.001$) and type of insect trap ($F_{1,19} = 1.9$, $P = 0.19$). This lack of significant association was also evident within our two sites with the most data: New York ($b = 0.10 \pm 0.07$; $r^2 = 0.22$, $n = 11$ site-years, $P = 0.15$) and Wisconsin ($b = -0.08 \pm 1.0$; $r^2 = 0.08$, $n = 9$ site-years, $P = 0.45$). There was also no significant association between the 25th percentile of laying dates and the seasonal peak of food abundance when we used a 5-d running average of insect biomass ($b = 0.05 \pm 0.08$; $r^2 = 0.01$, $n = 26$ site-years, $P = 0.56$). The date of peak insect biomass as estimated by this 5-d running average was highly correlated with the date estimated using a single day ($r^2 = 0.88$, $n = 26$ site-years, $P < 0.001$).

The average date of laying was also not associated significantly with the seasonal peak of food abundance ($b = 0.06 \pm 0.05$; $n = 26$ site-years, $P = 0.27$) in a model that included study site ($F_{4,19} = 11.0$, $P < 0.001$) and type of insect trap ($F_{1,19} = 1.7$, $P = 0.21$). When we examined our two long-term sites, the only trend we detected was in New York, where the mean date of laying tended to be later when the date of maximum insect biomass was later ($b = 0.09 \pm 0.05$; $r^2 = 0.32$, $n = 11$, $P = 0.07$). This relationship was nonsignificant in Wisconsin ($b = -0.06 \pm 0.06$; $r^2 = 0.06$, $n = 9$, $P = 0.52$). The average date of peak insect biomass was 5 June (± 3.36 d; range: 2 May to 26 June, $n = 26$ site-years), and the average number of days between the mean laying date and date of peak insect biomass was 14.8 ± 3.45 d ($n = 26$ site-years).

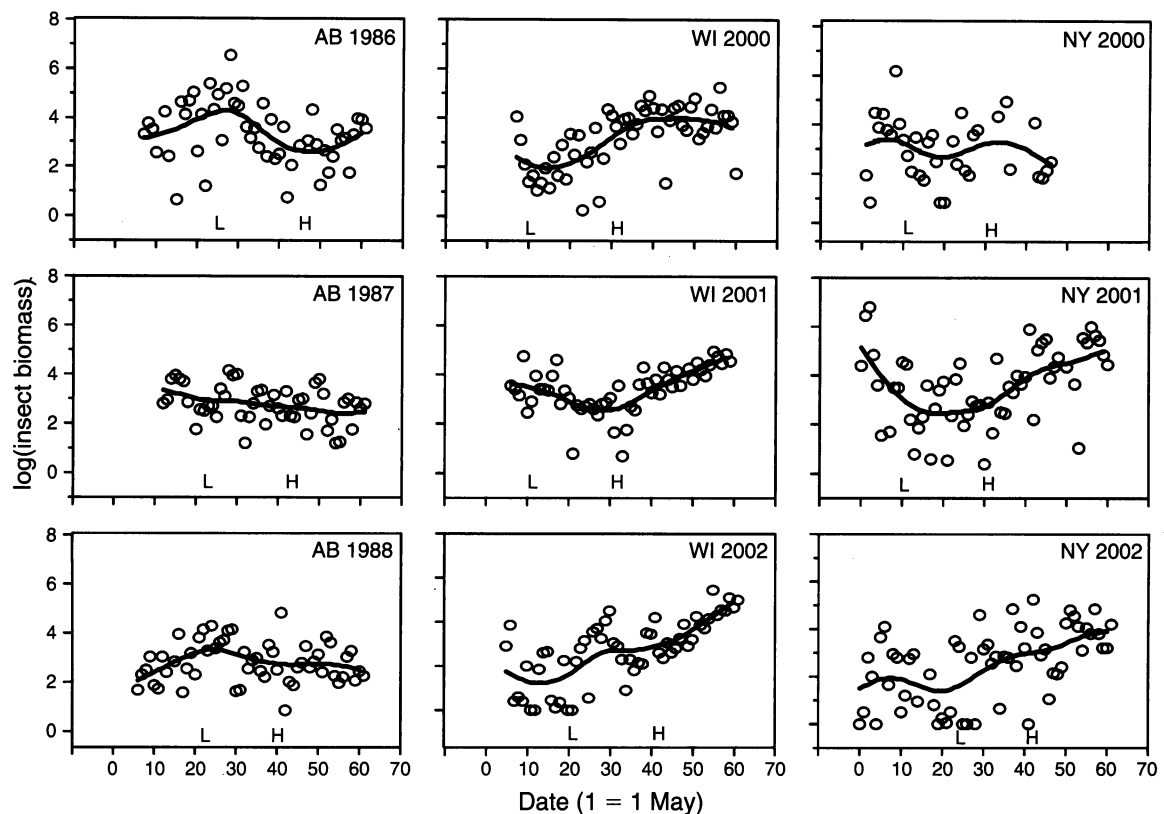


FIG. 1. Examples of seasonal patterns of log-transformed insect biomass (originally measured in mg) in relation to mean laying (L) and hatching (H) dates of Tree Swallows (*Tachycineta bicolor*). Dates are numbered consecutively: 1 = 1 May. Lines are cubic splines. Insect biomass is from tow nets in Alberta (AB), and suction traps in Wisconsin (WI) and New York (NY). Data from other years are in Appendix B.

Mean hatch dates were also not related significantly to the timing of peak insect abundance ($F_{1,19} < 0.1$, $P = 0.84$; model also included site [$F_{4,19} = 8.8$, $P < 0.001$] and year [$F_{1,19} = 0.4$, $P = 0.53$]), because the peak date of insect abundance was highly variable. The average date of hatching was 10 June (± 1.21 d), so birds hatched 4.8 d (± 3.55 , $n = 26$) after the peak of insect abundance (range: 19 d before to 33 d after; $n = 25$ site-years; Fig. 1; Appendix B: Fig. B1, 2). Mean hatching date barely changed (9 June ± 0.80 d, $n = 25$ site-years) when we excluded Yellowknife, but the range was reduced from 30 to 16 days. Indeed, hatching dates were remarkably invariable (CV = 10.2%) compared to the date of peak insect abundance (CV = 48.8%; without Yellowknife), and there was no correlation between them ($r = -0.08$, $n = 25$ site-years, $P = 0.69$). The difference in timing of hatch and peak of food abundance varied between sites ($F_{3,19} = 5.0$, $P = 0.01$), but was not related to year ($F_{1,19} = 1.5$, $P = 0.24$) after controlling for type of insect sampler ($F_{1,19} = 13.5$, $P = 0.002$). Hatching generally occurred after the peak of insect abundance in Alberta (least squares mean: 0.8 ± 11.0 d, $n = 3$) and New York (31.6 ± 7.5 d, $n = 11$), while it was before the peak in Ontario (13.0 ± 11.7 d, $n = 2$) and Wisconsin (3.7 ± 6.56 d, $n = 9$).

Over the 24 years of our study (1986–2009), the interval between mean hatching date and peak insect abundance has not changed significantly because there has not been any change at our study sites in the mean laying date (year effect, $F_{1,20} = 0.6$, $P = 0.44$; site, $F_{4,20} = 11.6$, $P < 0.001$), hatch date (year effect, $F_{1,20} = 0.4$, $P = 0.52$; site, $F_{4,20} = 9.4$, $P < 0.001$), or date of peak food abundance (year effect, $F_{1,19} = 1.6$, $P = 0.21$; site, $F_{4,19} = 3.8$, $P = 0.02$; type of insect sampler, $F_{1,19} = 12.2$, $P = 0.002$). Note that our longer-term analysis (1958–1992) of nest-record cards (Dunn and Winkler 1999) showed a change in laying date, because there was later laying in the 1960s and 1970s (Fig. 1a in Dunn and Winkler 1999).

Assumption 2: Selection for synchrony between laying and peak food abundance

Contrary to the assumption of the mismatch hypothesis, there was little evidence that selection favors birds that synchronize their laying date with the seasonal peak of food abundance. Neither linear nor quadratic selection gradients (Appendix A: Table A2) were related significantly to the interval between mean laying date and the date of peak insect biomass (Fig. 2). However, as found in other studies, birds produced more fledglings

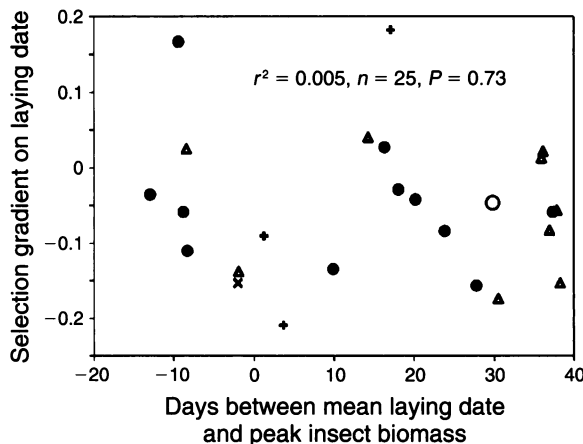


FIG. 2. Selection gradients on laying date in relation to synchrony between timing of laying and peak of insect abundance. Selection gradients were based on regressions for each site and year in Appendix A: Table A2. Key to symbols: crosses (+), Alberta; solid circles (●), New York; x, Northwest Territories; open circle (○), Ontario; triangles (Δ), Wisconsin.

when they laid earlier, and, thus, there was significant directional selection for earlier laying (Table 2). However, the strength of this selection was weak, because little of the variation in fledging success was explained by laying date ($r^2 = 0.004$; Table 2). On closer examination of the data, the weak selection was not surprising, because only five of 27 site-years showed a significant relationship between relative fledging success and standardized laying date (4/5 were negative) and, thus, a significant selection gradient (Appendix A: Table A2). Four site-years showed significant quadratic selection on laying date, and three of these were negative, suggesting stabilizing selection (Appendix A: Table A2). The main reason for the weak selection on laying date was a weak relationship between clutch size and number of eggs that hatched. A path analysis indicated that there was a strong negative relationship between laying date and clutch size (partial regression coefficient: $b' = -0.36$), but laying date was not strongly related to the number of eggs that hatched ($b' = -0.027$) or the subsequent number of fledglings ($b' = 0.08$).

Assumption 3: The timing and abundance of food for offspring is predictable early in the season

The third assumption of the mismatch hypothesis is that the timing and abundance of food during the nestling period is predictable from conditions prior to laying. At our study sites, the date of peak insect biomass was earlier when temperatures were higher during 1–5 May ($b = -2.28 \pm 0.93$, $R^2 = 0.57$, $F_{1,19} = 6.1$, $P = 0.003$, $n = 25$ sites) and insect abundance was greater during 6–10 May ($b = -12.5 \pm 3.35$, $R^2 = 0.71$, $F_{1,16} = 14.0$, $P = 0.002$, $n = 22$ sites) in models that included site and type of insect sampler. Thus, swallows could potentially use these environmental cues to time their laying so the energetic demands of nestlings are synchronized with peak food abundance. However, as shown previously, they apparently do not do so, as the dates of laying and hatching were not related significantly to the date of peak food abundance.

In contrast, the abundance of food during the nestling period was not predictable. Insect biomass (log-transformed) during the nestling period was not related to temperatures or insect abundance during May (see variables in Table 1; all $P > 0.37$) in models that included type of insect sampler and site. It is possible that temporal changes in insect abundance during the laying period of the population (25th to 75th percentiles of laying dates) might provide cues to when insects will be abundant later in the season, but there was no regular change in insect abundance with date during the laying period ($F_{1,146} = 1.47$, $P = 0.22$; model also included type of insect sampler, year, and site; overall $R^2 = 0.35$, $F_{20,146} = 4.5$, $P < 0.001$). Results were qualitatively similar ($F_{1,353} = 0.05$, $P = 0.82$) using the 10th to 90th percentiles of laying dates to define the laying period; note that using this range increased the number of sampled days from 167 to 376 (Appendix A: Table A1). Thus, there are some environmental cues during laying that could provide reliable cues to females about the timing, but not the abundance, of food that will be available to nestlings.

DISCUSSION

Although there is widespread evidence of shifts in breeding phenology (Parmesan and Yohe 2003), it is not

TABLE 2. Selection gradients on laying date (standardized by site and year).

R^2	Laying date (linear)				(Laying date) ² (quadratic)			
	b	SE	F (df)	P	b	SE	F (df)	P
0.004	-0.042	0.013	11.0 (1, 2896)	<0.001				
0.004	-0.030	0.015	3.9 (1, 2895)	0.048	-0.009	0.007	2.18 (1, 2895)	0.14

Notes: The dependent variable was relative fledging success, and the predictors were standardized laying date (first model) or standardized laying date and (laying date)² (second model). Relative fledging success was the number of fledglings at a nest divided by mean success for each year and location. There was only evidence of directional selection on laying date (first model) as the quadratic (nonlinear) term was not significant in the second model. Analysis only included nests with complete information on laying date, clutch size, and the number of eggs hatched and young fledged. Samples included Alberta ($n = 161$ nests), Ontario ($n = 325$), New York ($n = 1868$), and Wisconsin ($n = 544$).

TABLE 3. Studies of the mismatch hypothesis and the predictability of food abundance during the breeding season.

Predator species	Prey type	Selection on timing of breeding in relation to food?	Young produced at peak food abundance?
Mismatch hypothesis supported			
Atlantic cod, <i>Gadus morhua</i> †	copepod	yes	yes
Thick-billed Murre, <i>Uria lomvia</i>	fish	yes	yes
Blue Tit, <i>Cyanistes caeruleus</i>	caterpillars	yes	yes
Great Tit, <i>Parus major</i>	caterpillars	yes	yes
Pied Flycatcher, <i>Ficedula hypoleuca</i>	caterpillars	yes	yes
Geometrid moth, <i>Operophtera brumata</i>	oak	yes	yes
Daphnia, <i>Daphnia pulicaria</i> ‡	diatom	yes	no
Rhinoceros Auklet, <i>Cerorhinca monocerata</i>	anchovy	yes	no
Rhinoceros Auklet, <i>Cerorhinca monocerata</i>	anchovy	yes (exp.)	ND
Marine bivalve, <i>Macoma balthica</i>	phytoplankton	yes	no
Threadfin shad, <i>Dorosoma petenense</i>	zooplankton	yes	no
Cassins's Auklet, <i>Ptychoramphus aleuticus</i>	fish	yes (exp.)	ND
Haddock, <i>Melanogrammus aeglefinus</i>	phytoplankton	yes	ND
Montagu's Harrier, <i>Circus pygargus</i>	voles	ND	ND
Mismatch hypothesis not supported			
Tree Swallow, <i>Tachycineta bicolor</i>	aerial insects	no	no
House Wren, <i>Troglodytes aedon</i> §	insects	no	no
Common Murre, <i>Uria aalge</i>	fish	no	no
Black-legged Kittiwake, <i>Rissa tridactyla</i>	fish	no	no
<i>Keratella</i> , <i>Keratella cochlearis</i> ‡	diatom	no	yes
Soay sheep, <i>Ovis aries</i> †	grass	no	ND
Atlantic Puffin, <i>Fratercula arctica</i> †	fish	no	ND
Mallard, <i>Anas platyrhynchos</i>	chironomids	ND	no
Widgeon, <i>Anas penelope</i>	chironomids	ND	no
Eurasian Teal, <i>Anas crecca</i>	chironomids	ND	no
Arctic cod, <i>Boreogadus saida</i>	copepod	ND	no
Sand lance, <i>Ammodytes</i> sp.	copepod	ND	no
Keelback snake, <i>Tropidonophis mairii</i> ¶	frogs	ND	no

Note: ND indicates that no data were available, and "(exp.)" indicates results of experimental studies.

† Fitness in sheep and puffin populations was only related to the abundance of food and not to the timing of food (mismatch); whereas cod abundance was related to both timing and abundance of food.

‡ Selection from mismatching is apparently driving a long-term decline in *Daphnia*, but there is no apparent selection on *Keratella*, even though it tracks diatom abundance. This difference may be occurring because *Keratella* and diatom densities are correlated with water temperature, but *Daphnia* densities are not correlated.

§ Food abundance for wrens was either relatively constant year-round or peaked months before or after the breeding season.

¶ Nesting occurs in May and June when soil moisture and temperatures are optimal for incubation; food abundance (frogs) does not vary seasonally.

clear whether these shifts are necessary or sufficient to keep pace with shifts in food supply caused by climate change (Visser and Both 2005). Based on analysis of nest record cards from across the breeding range, Tree Swallows have advanced their mean date of laying by about 9 days since the late 1950s (Dunn and Winkler 1999). However, there was no evidence from our study sites that selection favors swallows that synchronize their time of laying with a peak in food abundance later in the season. Although the timing of peak food abundance was predictable early in the season from temperature and food abundance in early May, females apparently did not use these cues, as the dates of laying and hatching were not related to the date of peak food abundance. In contrast to the timing of food, its abundance during the nestling period of Tree Swallows

was unpredictable, and there was no significant selection on timing of laying to match the peak of food abundance. Thus, at best, only one of the assumptions of the mismatch hypothesis was supported by our study. In general, the start of laying in Tree Swallows was related to food abundance during the laying period ($P = 0.02$), and not to timing of the seasonal peak in food supply ($P = 0.26$; Table 1). Thus, it is unlikely that selection on timing of laying occurs as a consequence of mismatches with food supply during the nestling period. There is selection on timing of laying, but it occurs because birds that lay earlier generally have larger clutches and fledge more offspring (Table 2), and the decision to lay early is primarily influenced by conditions during the laying, and not the nestling, period. To date, studies seem evenly divided in their support for the

TABLE 3. Extended.

Peak food abundance predictable at beginning of season?	Sources
yes	Cushing (1990), Beaugrand et al. (2003), Durant et al. (2005)
yes	Gaston et al. (2009)
yes	Blondel et al. (1993), Thomas et al. (2001), Bourgault et al. (2010)
yes	van Noordwijk et al. (1995), Visser et al. (1998), Charmantier et al. (2008)
yes	Both and Visser (2001), Sanz et al. (2003), Both and Visser (2005)
yes	Tikkanen and Julkunen-Tiitto (2003), Tikkanen et al. (2006)
yes	Winder and Schindler (2004)
no	Watanuki et al. (2009)
ND	Hipfner (2008), Hipfner et al. (2008)
no	Philippart et al. (2003)
ND	Betsill and van den Avyle (1997)
ND	Hipfner et al. (2010)
ND	Platt et al. (2003)
yes	Salamolard et al. (2000), Millon et al. (2008)
yes (timing), no (abundance)	see <i>Results</i>
no	Young (1994)
yes	Shultz et al. (2009)
yes	Shultz et al. (2009)
yes	Winder and Schindler (2004)
ND	Durant et al. (2005)
ND	Durant et al. (2005)
no	Dessborn et al. (2009)
no	Dessborn et al. (2009)
no	Dessborn et al. (2009)
no	Fortier et al. (1995)
no	Fortier et al. (1995)
no	Brown and Shine (2006)

mismatch hypothesis, but some general patterns emerge from examining its assumptions (Table 3).

The first assumption of the mismatch hypothesis is that the period of food availability is short relative to the needs of offspring, which may occur if the food supply is declining later in the season. It is this limited availability that leads to strong selection for matching the timing of reproduction with food supply. At our study areas, food abundance generally increased during the nestling period, as well as across the entire breeding season, but it was also variable, as only half of the site-years showed a steady linear increase over the season. There is probably a decline of aerial insects later in the summer (August or September), as has been found in barn swallows (Grüebler and Naef-Daenzer 2008), but it would occur after Tree Swallows have left the breeding grounds (mid- to late July).

There is general support for the mismatch hypothesis in species that produce their young at the seasonal peak in food abundance (six of 10 species; Table 3). Most of the exceptions occur when young are produced well before any peak in food abundance, as has been described for some fish (Fortier et al. 1995), bivalve

(Philippart et al. 2003), and zooplankton (Varpe et al. 2007) species. In these cases, young may be selected for an earlier start because predation or developmental constraints (e.g., timing of metamorphosis, molt, or migration) exert stronger selection than food availability. In some cases, abiotic factors may also have a stronger influence on the timing of reproduction than food abundance. For example, in northern Australia, food (frog) abundance for keelback snakes (*Tropidonophis mairii*) does not vary significantly over the year, but snakes show a seasonal peak of egg-laying in May–June when soil temperature and moisture are optimal for incubation (Brown and Shine 2006). Support for the mismatch hypothesis is also weaker in environments with relatively constant or abundant food throughout the breeding season because there is no clear peak in food abundance. This appears to be the case with Tree Swallows, as well as Reed Warblers (*Acrocephalus scirpaceus*), which live in marshes that have superabundant food throughout the nestling period (Halupka et al. 2008).

The second assumption of the mismatch hypothesis is that selection favors individuals that synchronize their timing of reproduction with the peak of food abundance. If so, then we predict that they will have greater fitness, as estimated by offspring growth, number of independent young, and recruitment. Relatively few studies have examined this prediction because it requires detailed information about the timing of both reproductive success and prey abundance (Table 3). It is worth noting that Table 3 excludes some studies because they examine food abundance across the entire season and do not address timing with particular stages of reproduction. Overall, most studies (13 of 20) indicate that there is significant selection on timing of reproduction in relation to timing of food abundance (Table 3). However, it is often not clear if this selection is caused by mismatching per se or directional selection for earlier reproduction for other reasons, such as larger clutches or more time for offspring to develop. Tree Swallows appear to be an example of the latter, as laying dates have advanced over the long term (1958–1992) despite a lack of selection specifically related to mismatching. Another potential problem with testing this hypothesis is that fitness is influenced by the quality of offspring, and so early eggs (Varpe et al. 2007), which are often produced by older or more experienced parents in iteroparous species, may have greater reproductive value and contribute more to population recruitment (Nager and van Noordwijk 1995, Grieco et al. 2002).

Although much attention has focused on the mismatch hypothesis, the absolute level of food abundance and its distribution throughout the breeding season may also have an important effect on reproductive success. For example, recruitment in three different predator or herbivore systems (cod/zooplankton, puffin/herring, and sheep/vegetation) indicated that survival was primarily related to the abundance of food, and less so to the



PLATE 1. Tree Swallows are aerial insectivores strongly affected by weather during egg-laying. Photo credit: D. W. Winkler.

degree of mismatch (Durant et al. 2005). A broader life-history perspective suggests that timing of reproduction will be influenced by the variance of food availability, which will influence the degree of mismatch, the level of competition for territories, and the risk of mortality to adults from starting to breed "too early" when environmental conditions may be severe (Jonzén et al. 2007). Thus, some species, such as Tree Swallows, may not incur a large fitness cost from mismatches because the food supply is abundant or without a strong seasonal peak.

The third assumption of the mismatch hypothesis is that individuals can predict the time of peak food supply from conditions at the start of breeding. Although there are many food supplementation studies showing that food supply influences the decision to lay, it is often not clear whether this is a response to an energetic constraint on forming eggs or an adaptive decision based on the timing of food for offspring. In some cases, it appears that food supplies after hatch are either unpredictable

on the basis of conditions prior to laying (Eeva et al. 2000, Török et al. 2004) or not related to reproductive performance (Nol 1989). Hussell and Quinney (1985) examined eight years of data from Tree Swallows breeding at three sites in Ontario and also concluded that females could not predict food abundance during the nestling period on the basis of food abundance during laying (at least within sites). Thus, timing of laying in Tree Swallows appears to be based primarily on the current rate of food intake for egg production (Winkler and Allen 1996, Nooker et al. 2005), rather than the food supply during the nestling period. Indeed, we found that birds laid earlier when food abundance before laying was higher, as has been suggested by our studies that have handicapped females and, thereby, reduced their foraging efficiency (Winkler and Allen 1995, Nooker et al. 2005). Note that these conclusions are based on relatively fine-scale (day to week) analyses of laying dates and food abundance. At a broader level, it might be argued that breeding is timed to coincide

with seasonal (monthly) levels of food abundance (e.g., insect abundance is 1.6 times greater in June when nestlings are being fed than in May when laying begins). Indeed, there is evidence from another aerial insectivore, the House Martin (*Delichon urbica*), that the timing of laying generally coincided with the time of year when food was most abundant (Fig. 17 in Bryant 1975). However, House Martins have two broods per season, which leads to a long breeding season (May to September) and that analysis used monthly mean values for the food supply, so a positive relationship is not unexpected.

Evidence for more precise coordination of breeding comes from studies of songbirds in western and central Europe in which clutches of eggs often hatch in synchrony with the peak of one key food source for nestlings (winter moth caterpillars). For example, in three species of tits and Pied Flycatchers breeding in the Netherlands (Both et al. 2009), variations in hatch date were relatively large (mean CV = 23%) compared to Tree Swallows (CV = 10%), and the Dutch birds changed their date of hatch by an average of 0.49 d (± 0.06) for every day of change in their caterpillar prey. In contrast, Tree Swallows changed (nonsignificantly) their date of hatch by 0.02 d (± 0.05) for every day of change in the peak of insects. Note that, in contrast to passerines in northern European forests, swallows feed their young on a diverse set of aerial insects. They also arrive on the breeding grounds weeks before laying begins, and, thus, their lack of synchrony with the food supply cannot be attributed to a late arrival on the breeding grounds, as has been suggested for Pied Flycatchers (Both and Visser 2001). It should also be noted that some other populations of tits and Pied Flycatchers do not appear to adjust the time of hatch with the peak in food abundance. For example, in northern Finland, insect abundance is greatest in July and August after the nestling period of most passerines, including Great Tits and Pied Flycatchers (Eeva et al. 2000).

Conclusions

As global temperatures increase, concern has been raised about the ability of seasonally breeding organisms to adapt to changes in the timing of their food supply. The response of these organisms will depend on whether they can use environmental conditions early in the season to adjust their timing of reproduction and how changes in phenology ultimately affect their fitness. Although many studies discuss the effects of food, or more recently temperature, in the context of climate change or the seasonal decline in clutch size, rarely do they measure naturally occurring levels of food during the laying and nestling periods. Studies that supplement food supplies are valuable, but they also rarely differentiate between food supplemented during the laying (or gestation) and offspring periods, so it is not clear how the timing of food relates to selection on timing of reproduction. Our study emphasizes the need

to know how natural levels of food abundance relate to reproductive success at both the laying and nestling stages. Contrary to the well-studied tits and flycatchers of Europe, we found that food supply during the laying period was most important to reproductive success, and mismatches with food supply during the nestling period had little selective importance.

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APPENDIX A

Tables showing regression analyses of insect biomass in relation to date during the laying and nestling periods and selection gradients on standardized laying date for each year and location (*Ecological Archives* E092-039-A1).

APPENDIX B

Figures showing seasonal patterns of insect biomass from Alberta, New York, Northwest Territories, Ontario, and Wisconsin (*Ecological Archives* E092-039-A2).

SUPPLEMENT

Dates of laying, hatching, and peak insect biomass used in Table 1 (*Ecological Archives* E092-039-S1).