Can changes in provisioning by parent birds account for seasonally declining patterns of offspring recruitment?

L.E. Bortolotti, V.B. Harriman, R.G. Clark, and R.D. Dawson

Abstract: Declining reproductive success among individuals that breed later in the season occurs in numerous taxa and is particularly well-documented in birds. Principal ideas advanced to explain this pattern, the date and parental quality hypotheses, consider the ultimate causes of this phenomenon and have received much attention; however, proximate mechanisms have not been clearly elucidated. Parental provisioning could mediate a seasonal decline in nestling fitness. We delayed hatch dates and manipulated brood sizes of Tree Swallows (Tachycineta bicolor (Vieillot, 1808)) to assess the ability of parents to compensate for deteriorating environmental conditions and increased demands of more chicks. We measured provisioning rates using audio recordings of nestlings begging. Brood size was the best predictor of provisioning frequency, with parents feeding larger broods more frequently than smaller ones. Delayed hatching did not reduce provisioning rate despite declining food abundance. Date and food abundance were unrelated to provisioning rate, suggesting no seasonal change in the quantity of food nestlings receive. However, provisioning frequency was informative about life-history strategies of Tree Swallows, showing that late breeders incurred the costs of deteriorating environmental conditions rather than passing these costs on to their offspring.

Résumé : Il se produit un succès reproductif réduit chez les individus qui se reproduisent plus tard en saison chez de nombreux taxons et le phénomène a été particulièrement bien étudié chez les oiseaux. Les théories principales avancées pour expliquer le phénomène, les hypothèses de la date et de la qualité des parents, considèrent les causes ultimes et ont été bien étudiées ; les mécanismes proximaux n’ont cependant pas été clairement élucidés. L’approvisionnement parental pourrait expliquer un déclin saisonnier de la fitness des petits au nid. Nous avons retardé les dates d’éclosion et manipulé les tailles des couvées chez des hirondelles biclores (Tachycineta bicolor (Vieillot, 1808)) afin d’évaluer la capacité des parents à compenser la dégradation des conditions du milieu et les besoins accrus d’un nombre plus grand de petits. Nous avons mesuré les taux d’approvisionnement à l’aide d’enregistrements audio des cris de sollicitation des petits au nid. La taille de la couvée est la meilleure variable prédictive de la fréquence des approvisionnements et les parents alimentent plus fréquemment les couvées plus grandes que les plus petites. L’éclosion retardée ne réduit pas le taux d’approvisionnement malgré le déclin de l’abondance de nourriture. Il n’y a pas de relation entre la date et l’abondance de nourriture, d’une part, et le taux d’approvisionnement, d’autre part, ce qui laisse croire qu’il n’y a pas de changement saisonnier dans la quantité de nourriture reçue par les petits au nid. Cependant, la fréquence des approvisionnements renseigne sur les stratégies du cycle biologique des hirondelles biclores, en montrant que les oiseaux qui se reproduisent tardivement subissent eux-mêmes les coûts de la dégradation des conditions du milieu plutôt que de les transmettre à leurs rejetons.

[Traduit par la Rédaction]

Introduction

Declining reproductive success among individuals that breed later in the season has been observed in diverse taxa, including plants (Kelly and Levin 2000), arthropods (Cushman et al. 1994; Varpe et al. 2007), fish (Schultz 1993), mammals (Huber et al. 2001), and especially birds (Blums et al. 2002; Rossmanith et al. 2007). In many avian species, nestling mass and growth rate (e.g., Sedinger and Flint 1991; Wardrop and Ydenberg 2003), fledging success (e.g., Verhulst et al. 1995; Dawson 2008), and recruitment (e.g., Hochachka 1990; Shuter et al. 2006) decrease with later hatch date. This pattern can be attributed to numerous putative causes, including low-quality individuals breeding later in the season (parental quality hypothesis; Price et al. 1988), deteriorating environmental conditions later in the breeding sea-

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son (date hypothesis; Perrins 1970), or some combination of these factors. Parental quality refers to the phenotypic condition of parents or the quality of territory they hold (Siikamäki 1998; Verhulst and Nilsson 2008) so that birds breeding at the same time should be of comparable quality. The date hypothesis encompasses factors such as variation in weather, intensity of parasitism, and food quantity (often cited as the most important factor; Siikamäki 1998). Despite numerous studies having investigated these two hypotheses (reviews in Arnold et al. 2004; Verhulst and Nilsson 2008), the proximate factors causing a seasonal decline in reproductive success have not been adequately resolved.

Variation in nesting quality and reproductive success may be explained by parental food provisioning, which is mediated by parental behavioral decisions or environmental constraints on parents (Nur 1984; Ardia 2007). Provisioning rate influences nestling mass and growth (Shutler et al. 2006; Ardia 2007), which are important to nestling health and survival (McCarty 2001). Yet, parental provisioning rates may decline over the breeding season and it is unknown to what degree parental care could account for seasonally declining reproductive success.

To investigate parental provisioning in relation to timing of breeding, we studied Tree Swallows (Tachycineta bicolor (Vieillot, 1808); hereafter swallow), a migratory, aerial insectivore that raises only one brood per breeding season. Because of the timing of insect emergences, swallows experience short-term fluctuations in food supply (McCarty 2001), with altricial young being fed by parents for approximately 20 days posthatching (Robertson et al. 1992). Swallows are an ideal model species for studying provisioning rates because they are resilient to human disturbance, readily breed in nest boxes (Robertson et al. 1992), and the number of visits by adults to the nest box is a reliable measure of feeding rate (McCarty 2002; Whittingham et al. 2003). Prey selection by swallows is consistent during the nesting period, despite changes in environmental conditions and insect availability (McCarty and Winkler 1999), and there is little variation with date in the amount of food (i.e., bolus size) delivered (Quinney 1986; McCarty 2002). In addition, both fledging success and recruitment probability (i.e., the probability that a nestling will survive, return to its natal population, and be recaptured) typically decline with laying date in swallows (Shutler et al. 2006; Dawson 2008; details below in the Materials and methods).

Here, our main objective was to undertake concurrently two experimental manipulations: delay of hatch date and brood-size manipulation. If declining provisioning rate proximately drives seasonally declining reproductive success of swallows, then under both the parental quality and date hypotheses we would predict that provisioning rate would decline seasonally, ultimately driven by declining quality of breeding pairs (parental quality hypothesis), deteriorating environmental conditions (e.g., food abundance; date hypothesis), or a combination of the two factors. By delaying hatch date of some birds, we were able to separate effects of differences in parental quality related to timing of breeding from the behavioral responses of parents to environmental variability. Specifically, the date hypothesis predicts that delayed pairs will provision less frequently than control birds, whereas the parental quality hypothesis predicts that they will provision at the same frequency as control birds. Brood-size adjustments provided a means of testing the ability of parents to compensate for increased food demands. In general, we predicted that early-breeding individuals would be better able to cope with brood enlargement than late-breeding individuals, owing to either more favorable environmental conditions or superior parental quality.

Materials and methods

General methods

Work was conducted at the St. Denis National Wildlife Area (NWA; 52°N, 106°W), ~40 km east of Saskatoon, Saskatchewan, Canada, and at a site near Prince George, British Columbia, Canada (PG; 53°N, 122°W), during May–August 2008. Swallow populations at the NWA and PG experience different environmental conditions during the breeding season; thus, experiments conducted on these sites represent true replication (versus working for 2 years at one site). Swallows nested in wooden boxes placed 1.5 m above the ground, attached either to metal (NWA) or fence (PG) posts spaced ≥30 m apart. There were 202 and 122 nest boxes at the NWA and PG, respectively. Nesting material was removed from boxes at the end of each breeding season. When most eggs in a clutch had hatched, adult birds were trapped, banded, weighed, and wing chord and head–bill lengths were measured. Detailed descriptions of the sites are given by Shutler and Clark (2003; NWA) and Dawson (2008; PG). The following protocol was approved by the University of Saskatchewan’s Animal Care and Use Committee (protocol No. 20070041) and complied with current national and institutional ethics guidelines for animal care.

Nest monitoring and delay manipulation

Beginning in May, nest boxes were visited daily to determine clutch initiation and completion dates. Clutches were considered complete when clutch size was constant for three consecutive days. Each member of a pair of nests, matched for clutch initiation date, was randomly assigned to either the treatment (delay) or control group. In treatment nests, on the morning the third egg was laid, all three eggs were collected and replaced with solid plastic eggs (approximately 18 mm × 12 mm) that were painted white. Subsequent eggs were collected and replaced the morning that they were laid. Collected eggs were stored at 8 °C (Siikamäki 1998; Wiggins et al. 1994). The first four eggs laid were returned 3 days after clutch completion and the remaining 2–4 eggs were returned the following day to mimic natural hatching asynchrony. In control nests, eggs were removed from the nest cup, but immediately returned. Modal clutch size was 7 eggs at the NWA and 6 eggs at PG, for both the subsets of manipulated nests and the entire populations. Nests were visited periodically to determine hatching success and to trap adults (after ~14 days of incubation for control nests versus ~18 days for delayed nests), and to make audio recordings of nest activity.

At both sites, most clutches were initiated over a narrow range of dates. At the NWA, 99% of birds initiated clutches over a 13-day period (20 May to 1 June). The 58 nests included in our experiment were initiated over 12 days. At PG, 96% of swallows initiated clutches within an 11-day period (24 May to 3 June). Our experiment included 21 nests that
initiated over a 6-day period within those 11 days. Thus, a 4-day shift in timing of breeding represents 30% (NWA) and 36% (PG) of the principal part of the breeding seasons at the two sites. Based on long-term data from the NWA (Fig. 6 in Shutler et al. 2006), a 4-day delay in timing of breeding should produce a ~10% decline in probability of local recruitment. At PG, the proportion of nestlings fledged declined by ~6% for every day later that a brood hatched (based on data from Fig. 5 in Dawson 2008), so a 4-day delay would result in a ~22% decline in the proportion of offspring fledged.

**Brood-size manipulation**

Three nests that hatched on the same day, had the same clutch initiation date (within 1–2 days) and all belonged to either the delay or delay–control group, were randomly assigned to either brood enlargement, control, or reduction manipulations. Thus, there were six manipulation combinations: delay–enlargement (n = 11), delay–control (n = 11), delay–reduction (n = 13), control–enlargement (n = 13), control–control (n = 15), and control–reduction (n = 16). When nestlings were 2 days old, 2 nestlings from reduction nests were transferred to enlargement nests. Therefore, brood enlargement nests generally had 2 more nestlings than the number of eggs originally laid, brood reduction nests had 2 fewer nestlings, and control broods contained the same number of nestlings as eggs originally laid. On average, at the NWA, brood enlargement nests had 9 nestlings, control nests had 7, and reduction nests had 5. At PG, mean brood sizes were 7.5 (enlargement), 5.5 (control), and 4 (reduction). However, there was some deviation from this pattern because of natural hatching failure. Nestlings that were moved between nests were selected so that they were of intermediate mass in both the origin (reduction) and the destination (enlargement) broods. Nestlings in control nests were also weighed and then returned to their own nest.

Embryo mortality occurred in some delay manipulation nests (see also Wiggins et al. 1998). To achieve required brood sizes at the NWA, nestlings from two to four different nests of the same age were used to create some broods. At PG, which had less embryo mortality, composite broods were not used.

**Provisioning rates**

When nestlings were either 8, 10, or 12 days old, a microphone attached to an audio recorder (RCA model RP5030) was placed in the nest box to make hour-long recordings of nest activity. Recordings were made between 0900 and 1800. We used stratified random assignment of recording day so that each trio of nests (enlargement, reduction, control) had a nest recorded when nestlings were 8, 10, or 12 days old. Based on other behavioral studies of swallow provisioning (McCarty 2002; Shutler et al. 2006; Ardia 2007) and a preliminary study in 2007, we determined that analysis of the last 30 min of 1 h recordings provided a reliable estimate of parental provisioning rates and reduced presumed effects of the initial disturbance of placing the microphone in the nest box (L.E. Bortolotti, unpublished data). Recording nestlings between 8 and 12 days old encompasses the period of peak nestling growth (Zach and Mayoh 1982) and repeated measures analysis of 2007 pilot data showed no difference in feeding rates with respect to nestling age (P > 0.40). In addition, other studies have described the consistency of swallow provisioning rate (Shutler et al. 2006) and load size (McCarty 2002) throughout the nestling period. Analysis of recordings was done using Avisoft SASLab Light software (Avisoft Bioacoustics 1999). To verify that audio recorders can be used to monitor feeding visits by parent swallows, we observed 15 boxes (10 in 2007 and 5 in 2008) using a 20×–60× spotting scope from a position >50 m from the nest box while the audio equipment was operating. Overall, 99% of observed feeding visits (n = 160) were correctly identified from audio recordings. Recordings and observations were not made in the rain.

**Insect sampling**

Passive aerial insect samplers were erected at two locations at each of the NWA and PG sites. Data on wind speed were obtained from weather stations on each site. Sampling jars containing 95% ethanol were collected and replaced every 12 h at the NWA and every 24 h at PG. Samples were later dried and weighed (nearest 0.001 g on an Ohaus Analytical Plus scale). Values for daily insect abundance were obtained by adjusting insect biomass for sampling time and the mean wind speed during the sampling period. In addition to daily values, 2 and 3 day running cumulative insect biomass totals were calculated. Insect sampler set-up and drying protocols followed Quinney et al. (1986).

**Statistical analyses**

Analysis of covariance (ANCOVA, PROC GLM; SAS Institute Inc. 2003) was used to evaluate a priori hypotheses about the relationship between the number of visits to the box by adult swallows (i.e., provisioning rate) and brood manipulation, delay manipulation, and one or more ecologically relevant covariates related to attributes of parents (clutch size, female mass and size, male mass and size, and interactions between female attributes and manipulations), site effects (study site and interactions), characteristics of nestlings (number and age) and temporal factors (date and time of day). Least squares mean numbers of feedings (and 95% confidence intervals (CIs)) were calculated for treatment and control groups using the lsmeans option of PROC GLM. Provisioning rate was square-root-transformed to improve normality for analysis, but we present untransformed values for ease of interpretation. We considered 15 covariates and 37 models (12 are presented in Table 1), some of which included interactions between study site and delay treatment, site and number of nestlings, delay and brood manipulation, delay treatment and number of nestlings, and treatments and recording date. These interactions were considered because of possible site differences in ability of adults to provision nestlings resulting from site-specific differences in food abundance (Fig. 1) and weather conditions, or to consider explicit predictions. For these reasons, and because several environmental effects could not be adequately controlled in our field experiments, an information-theoretic approach to model selection was used. We followed criteria outlined in Burnham and Anderson (1998), wherein the model with the lowest sample-size-adjusted Akaike’s information criterion (AICc) is deemed to be best, and models...
Table 1. Ranking of models explaining variation in nestling provisioning rates by adult Tree Swallows (Tachycineta bicolor) at St. Denis National Wildlife Area, Saskatchewan, Canada, and Prince George, British Columbia, Canada, in June–July 2008.

<table>
<thead>
<tr>
<th>Model structure</th>
<th>RSS*</th>
<th>AICc ²</th>
<th>ΔAICc ³</th>
<th>wi ⁴</th>
<th>K ⁵</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nestlings (biological null)</td>
<td>77.21</td>
<td>5.98</td>
<td>0.00</td>
<td>0.179</td>
<td>3</td>
</tr>
<tr>
<td>Nestlings, Time</td>
<td>72.77</td>
<td>6.20</td>
<td>0.22</td>
<td>0.161</td>
<td>4</td>
</tr>
<tr>
<td>Delay, Nestlings, Time</td>
<td>71.36</td>
<td>7.82</td>
<td>1.84</td>
<td>0.071</td>
<td>5</td>
</tr>
<tr>
<td>Insects, Nestlings</td>
<td>75.91</td>
<td>8.08</td>
<td>2.10</td>
<td>0.063</td>
<td>4</td>
</tr>
<tr>
<td>Delay, Nestlings</td>
<td>76.97</td>
<td>8.10</td>
<td>2.12</td>
<td>0.062</td>
<td>4</td>
</tr>
<tr>
<td>Date, Nestlings</td>
<td>77.10</td>
<td>8.16</td>
<td>2.18</td>
<td>0.060</td>
<td>4</td>
</tr>
<tr>
<td>Area, Insects, Nestlings, Time</td>
<td>69.04</td>
<td>9.55</td>
<td>3.57</td>
<td>0.030</td>
<td>6</td>
</tr>
<tr>
<td>Brood Manipulation, CS</td>
<td>75.35</td>
<td>9.66</td>
<td>3.68</td>
<td>0.028</td>
<td>5</td>
</tr>
<tr>
<td>Brood Manipulation, CS, Time</td>
<td>71.46</td>
<td>10.22</td>
<td>4.24</td>
<td>0.022</td>
<td>6</td>
</tr>
<tr>
<td>Brood Manipulation</td>
<td>85.66</td>
<td>11.72</td>
<td>5.74</td>
<td>0.010</td>
<td>4</td>
</tr>
<tr>
<td>Brood Manipulation, Delay</td>
<td>85.63</td>
<td>14.00</td>
<td>8.02</td>
<td>0.003</td>
<td>5</td>
</tr>
<tr>
<td>Intercept only (statistical null)</td>
<td>105.21</td>
<td>14.30</td>
<td>8.32</td>
<td>0.003</td>
<td>2</td>
</tr>
<tr>
<td>Global model ¹</td>
<td>55.56</td>
<td>45.78</td>
<td>39.80</td>
<td>&lt;0.001</td>
<td>20</td>
</tr>
</tbody>
</table>

Note: Variables included were age of the nestlings when recorded (Age), study site (St. Denis or Prince George; Area), brood-manipulation category (Brood Manipulation), clutch size (CS), date of the recording day (Date), delay or control treatment (Delay), female head length (distance from the tip of the bill to the back of the skull of the parent female; F Head Length), mass of the parent female (F Mass), wing chord of the parent female (F Wing), insect biomass (sum of insect biomass on the day of recording and previous day; Insects), male head length (distance from the tip of the bill to the back of the skull of the parent male; M Head Length), mass of the parent male (M Mass), wing chord of the parent male (M Wing), number of nestlings in each box (Nestlings), and time of day of recording (Time).

²Residual sum of squares.
³Akaike’s information criterion corrected for small-sample bias is an estimator of the expected Kullback–Leibler information (i.e., the discrepancy between the candidate model and the true model generating the data).
⁴The difference between AICc of the candidate model and the minimum AICc (5.98).
⁵Akaike weight is the likelihood that the candidate model is the best model in the set, given the data and the other models in the set.
⁶K is the number of estimable parameters.
⁷Covariates and interactions included were Age, Area, CS, Date, Delay, F Head Length, F Mass, F Wing, Insects, M Head Length, M Mass, M Wing, Nestlings, Time, Area × Delay, Area × Nestlings, CS × Nestlings, and Delay × Nestlings.

with ΔAICc values ≤2 and <4 (ΔAICc being the difference between the best-approximating and lower ranked models) are considered well-supported and plausible, respectively. Akaike weights (wi) were also used to make inferences about relative support for competing models (Johnson and Omland 2004).

Results

The global model, which contained manipulation covariates and potentially ecologically significant variables and interactions, received little support (Table 1). More parsimonious models excluded attributes of parents, nestling age, and interactions. Of the measures describing conditions on the days of recording (i.e., date, insect biomass, 2- or 3-day running totals of insect biomass), the 2-day running total of insect biomass had the greatest explanatory power. Although insect biomass did not appear in any of the top models, it was a covariate in several of models with some plausibility (i.e., ΔAICc < 4; Table 1).

Parental provisioning was most strongly influenced by the number of nestlings in the brood (Table 1). The number of nestlings appeared in all of the best-approximating models, whereas models with related variables (i.e., brood-size manipulation and clutch size, substituted for number of nestlings) had comparatively little support. Parents increased feeding frequency at nests containing more nestlings (Fig. 2). The importance of the number of nestlings was reflected by the feeding rates within the different brood-manipulation categories. The number of feedings per 30 min, accounting for the effects of time of day and clutch size, was lower for reduced broods (lsmean = 5.4, 95% CI = 3.2–7.5) than for control (lsmean = 10.3, 95% CI = 8.1–12.6) and enlargement (lsmean = 12.6, 95% CI = 10.2–15.0) broods. Time of day was the only other variable to appear in the top models. Generally, feeding rates were higher in the afternoon than in the morning (β = 0.0011, SE = 0.0005).

Although delay treatment appears in one of the best-supported models, its effect was low relative to the top two models, as judged by low wi values (Table 1). Accounting for effects of time of day and brood-size manipulation, the least squares means of the feeding rate per half hour did not differ between delay (lsmean = 9.8, 95% CI = 7.9–11.8) and control (lsmean = 8.5, 95% CI = 6.8–10.3) groups.

Despite its link to number of nestlings, brood-size manipulation alone explained less variance in the number of feedings and so did not appear in any of the top models. Overall, the two types of manipulations did not greatly influence feeding rates, suggesting that parents were able to compensate for challenges related to the manipulation of both the timing of the nestling period and the number of nestlings.
Discussion

Provisioning and life-history strategy

Parental provisioning was strongly related to the number of nestlings in a brood (Fig. 2), consistent with the idea of a flexible reproductive investment strategy by adult Tree Swallows (see also Shutler et al. 2006; Ardia 2007). There was no evidence of a seasonal decline in provisioning (i.e., there were no date-influenced variables in the best-approximating models), despite a decline in food availability at the NWA during the period of time when behavioral data were collected (Fig. 1). The observation that delayed and control nests were provisioned at a similar rate further supports the lack of evidence for a seasonal decline in provisioning. If declining food resources forced a lower provisioning rate later in the season, delayed birds would have provisioned less than controls. In addition, PG had relatively low food abundance throughout the breeding season, yet site effects were absent from any of the top models. These findings differ from those reported in Blue Tits (Cyanistes caeruleus (L., 1758)), which experienced both a seasonal decline in provisioning and an increased provisioning effort by delayed parents (García-Navas and Sanz 2011). Our results suggest that parents compensate for poor environmental conditions by bearing costs themselves rather than passing them on to their offspring. Alternatively, it is possible that food supply was not limiting on either site. However, given that parents feeding enlarged broods did not provision significantly more than parents at control nests, there is some indication that the ability of parents to compensate declines with larger brood sizes (see also Nur 1984; Saino et al. 1997). In addition, measures of adult condition were not present in any top models, indicating that this strategy is not state-dependent with respect to this measure of parental quality (McNamara and Houston 1992). García-Navas and Sanz (2011) also observed no relationship between female mass and provisioning rate. According to life-history theory, energy allocation by parents involves a trade-off between the survival of parents and the survival of their offspring (Martin 1987). Given that swallows live, on average, 2.7 years and many females do not breed as yearlings, opportunities to breed could be limited (Robertson et al. 1992). That late breeders incur costs of deteriorating environmental conditions presumably reflects the high value of a brood to parent swallows.

It is important to examine the relative contribution of initial investment versus number of nestlings in determining the higher feeding rate in larger broods. Models that included both a measure of initial investment (clutch size) and brood size (manipulation) received less support than did models that included number of nestlings, suggesting that parents responded to the number of nestlings rather than to prior reproductive investment. Clutch size and number of nestlings were not tested in the same model because of obvious redundancy between the two variables.

Seasonally declining reproductive success

We did not observe an overall seasonal decline in provisioning, inconsistent with the hypothesis that decreasing rate of food provisioning is a proximate cause of seasonally declining reproductive success. Several other mechanisms could be responsible for the decline, many of which could be tested experimentally. First, although provisioning rate was not important, other aspects of provisioning could change seasonally. For example, late-reared nestlings may receive food of lower nutritional value. However, there is little pertinent information available on the nutritional value of insects (Robertson et al. 1992), making it difficult to evaluate the plausibility of this hypothesis. Ambient temperature is another environmental variable that influences nesting pheno-
type. Several studies have reported a positive relationship between temperature and nestling growth rate, plumage development, and immune response (McCarty and Winkler 1999; Dawson et al. 2005; Ambrosini et al. 2006). However, given that temperature generally increases or is stable during the breeding season, it alone cannot account for seasonal declines in reproductive success. An important caveat in any discussion of the influence of environmental factors on reproductive success is that interannual variation may alter the relative importance of the environment in any given year and may not produce consistent seasonal patterns. For example, at the NWA, weather during the breeding season in 2008 was relatively benign compared with 2007 when cold, rainy weather occurred when many early-nesting pairs had young nestlings (L.E. Bortolotti, personal observation). In such years, weather conditions may be a main source of nesting mortality or slow nestling growth, and could produce a pattern of seasonally increasing reproductive success. However, the pattern of seasonally declining reproductive success (nestling recruitment) observed at the NWA is highly consistent during the 17 years for which we have data (Shutler et al. 2006), and recent analyses indeed confirm that apparent first-year survival declines seasonally (V.B. Harriman, unpublished data). Thus, despite interannual variation, declining recruitment during the breeding season is a recurring pattern.

Parasitism may increase seasonally (de Lope and Møller 1993; Merino et al. 2000; O’Brien and Dawson 2008), reducing nestling condition and growth rate, or increasing anemia, virus transmission, and adverse effects on traits potentially related to fitness (Potti et al. 2007; Potti 2008; Tomás et al. 2008). Although ectoparasites and blood parasites did not affect nestling stress, growth, or fledging success at either the NWA or PG (Shutler et al. 2004; V.B. Harriman, unpublished data), interactions of two or more environmental factors may be responsible for seasonally declining reproductive success. Correct interpretation of our results hinges on key assumptions. A common criticism of experiments that delay the timing of hatching is that females in manipulated nests may have increased costs associated with longer incubation times (Verhulst and Nilsson 2008). However, incubation was extended by only 4–5 days, which in this study was insufficient to cause a change in female condition (V.B. Harriman, unpublished data). Secondly, parents may have been assisted in feeding nestlings by nonbreeding individuals. At the NWA, we occasionally observed birds other than the parents visiting active nests but we do not know if feeding frequency by these “nest attendants” was more common later in the breeding season, possibly reducing the workload and visits by parent birds, or whether they delivered much (if any) food. However, Lombardo (1986) found that Tree Swallow nest attendants did not feed nestlings and did not influence the reproductive success of the breeding pair. In addition, at the NWA, at least 96.3% of visits to the nest box are made by parents (R.G. Clark, unpublished data), and at PG, additional adults are rarely present at nests (R.D. Dawson, unpublished data).

Seasonally declining reproductive success, measured in terms of fledging success and recruitment, has been observed in multiple avian taxa including Passeriformes (Hochachka 1990; Verhulst et al. 1995; Siikamäki 1998; Verboven and Visser 1998; Naef-Daenzer et al. 2001; Shutler et al. 2006; Dawson 2008; Grüebler and Naef-Daenzer 2008; Delhey et al. 2010), Charadriiformes (Hatchwell 1991; Arnold et al. 2004; Hipfner et al. 2010), Anseriformes (Blums et al. 2002), Piciformes (Rossmanith et al. 2007), Falconiformes (Aparicio 1998), and Pelecaniformes (Childress and Bennun 2003). These groups have diverse life-history strategies, varying in characteristics such as duration of parental care, clutch size, number of broods raised, diet, and nesting strategy (e.g., colonial vs. solitary), and they occupy a large geographic span from the low-arctic (Common Murres, Urria aalge (Pontoppidan, 1763); Hatchwell 1991) to subsaharan Africa (Great Cormorants, Phalacrocorax carbo (L., 1758);Childress and Bennun 2003). It is therefore unlikely that any one factor is the proximate driver of seasonally declining reproductive success. For example, parental provisioning cannot be responsible for a decline in reproductive success in a species with precocial young. Additionally, seasonally declining recruitment may be influenced by processes (e.g., predation, starvation) that act after fledging, either on the breeding grounds, during migration, or on the wintering grounds (Sullivan 1989; Naef-Daenzer et al. 2001; Grüebler and Naef-Daenzer 2008), and these sources of mortality may intensify with date (Naef-Daenzer et al. 2001; Grüebler and Naef-Daenzer 2008). Multiple drivers of seasonally declining reproductive success likely act either singly or in concert, but operate differently in different species and years. Therefore, a conclusive and comprehensive identification of proximate drivers of seasonally variable reproductive success will require investigations of multiple species over multiple years.

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References


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McCarty, J.P. 2002. The number of visits to the nest by parents is an accurate measure of food delivered to nestlings in Tree Swallows. J. Field Ornithol. 73(1): 9–14.


