

**REPRODUCTIVE PERFORMANCE IN TREE SWALLOWS:
PROVISIONING, PARENTAL QUALITY AND SEASONAL
EFFECTS**

by

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Abstract

The goal of this thesis is to test two hypotheses for the ubiquitous seasonal decline in avian reproductive performance: either some variable associated with date *per se* determines performance (Date hypothesis); or later-breeding parents are of low quality and so perform poorly (Parent Quality hypothesis). I found that parent Tree Swallows (*Tachycineta bicolor*) breeding early in the season were better able to increase provisioning effort in response to experimentally increased brood demand, and that they produced larger nestlings than late breeders. To distinguish the two hypotheses, I manipulated hatch date by switching clutches among Tree Swallows breeding at Creston, British Columbia. I found that performance of manipulated broods during the first half of the season matched that predicted by the Date hypothesis, and in the second half matched that predicted by the Parent Quality hypothesis.

Several biases may make it difficult to detect parent quality effects. For example, hatch-date manipulations may (unintentionally) affect parent quality. I found that mass loss of incubating female Tree Swallows was reduced when hatch was advanced, but was unaffected when hatch was delayed. I also found significant heritability in mother-offspring tarsus length, as well as a maternal effect of egg size on day 4 nestling mass. None of these potential biases affect day 15 nestling mass, and seem unlikely to explain the observed support for the Date hypothesis. However, these and other biases need to be more carefully assessed in hatch-date manipulation experiments than has previously been considered.

I review previous studies of the seasonal decline in reproductive performance in other avian species, and find support for both the Date and Parent Quality hypotheses. The relative importance of their effects may depend on the life history of the species studied, climate, food abundance, or the biases described above.

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Table of Contents

Approval	ii
Abstract.....	iii
Acknowledgments	iv
List of Tables	ix
List of Figures	x
General Introduction.....	1
References.....	5
Chapter 1. Variation in provisioning ability of parent Tree Swallows ...	8
Introduction	8
Methods	9
Study area and breeding phenology.....	9
Parental Provisioning Response	10
Nestling characteristics	11
Results.....	12
Discussion.....	15
References.....	19
Chapter 2. Seasonal declines in reproductive performance: testing the date and parent quality hypotheses	21
Introduction	21
Methods	27
Study area and breeding phenology.....	27
Experimental Protocol	28
Parental Characteristics	29
Nestling mass.....	30

Statistical Analysis.....	30
Results.....	31
Characteristics of Treatment Groups.....	31
Hatching Difference.....	31
Impacts of the Experiment on Parent Quality.....	32
Discussion.....	37
References.....	40
Chapter 3. Sources of bias in hatch-date manipulation experiments ..	44
Introduction.....	44
Methods.....	48
Heritability.....	48
Statistical Analysis.....	49
Results.....	50
Heritability and Maternal Effects.....	50
Female Mass Loss.....	51
Discussion.....	56
Tarsus length.....	56
Egg size.....	57
Unintentional impacts of the experiment.....	60
Summary.....	62
References.....	63
Chapter 4. A literature review of hatch date manipulation experiments	67
Life History.....	69
Per offspring investment.....	69
Synchronous breeding.....	71
Territoriality of independent young.....	72

Trait studied.....	73
Variability in climate or food abundance	74
Unanticipated impacts of the experiment on parent quality.....	75
Conclusions.....	76
References	77
General Conclusions	82

List of Tables

Table 2.1. Characteristics of the 3 treatment groups. There is no statistical evidence of treatment differences in any of these variables. All variables were compared using ANOVA. Parameters are those of foster parents. Sample sizes are in parentheses. a = advanced, c = control, d = delayed.	33
Table 2.2. Multiple regression analysis of the variation in mean nestling mass. $R^2=0.297$, $n=38$. Hatching difference was not known for one brood. Correlation coefficients (r) were calculated using partial correlation analysis including mean nestling mass, hatch date and treatment.	34
Table 3.1: Backwards stepwise regression analysis of the variation in nestling mass at day 15 (M15), tarsus length at day 15 (TL) and nestling mass at day 4 (M4). Means were averages of broods. Non-significant variables ($p<0.10$) were dropped from the model. Model adjusted $R^2= 0.297$ (M15), 0.288 (TL) and 0.313 (M4). Correlation coefficients were calculated using a partial correlation analysis. Where F is blank, the variable was dropped from the analysis because $p>0.10$.....	52
Table 4.1: Summary of hatch date manipulation experiments. Numbers refer to individual studies, letters to multiple entries for a single study in the table.	68

List of Figures

- Figure 1.1. (a) Residuals of mean nestling mass (NM) on brood size and (b) mean structural size (PC1), are positively correlated with provisioning response (PR) (NM - $F = 5.19$, $p = 0.038$, $n=18$, $r=0.511$; PC1 - $F = 6.69$, $p = 0.02$, $n = 18$, $r = 0.501$). The regression equation for the lines are $NM = - 9.13 + 11.90 PR$. and $PC 1 = -6.84 + 9.30 PR$ 143**
- Figure 1.2: PR, measured as change in total brood mass/hour, declines with hatch date ($F = 9.41$, $p = 0.007$, $n = 18$, $r^2 = 0.331$). The equation for the line is $PR=1.149 - 0.009 \text{ Hatch Date}$ 14**
- Figure 2.1. Expected outcome of hatch-date manipulation experiments under the Date and Parent Quality hypotheses. Solid lines represent the natural seasonal trend, arrows indicate the direction of manipulation and the shaded area represents the predicted performance of manipulated broods. Panel A shows the predicted performance of manipulated broods under the Date hypothesis. Panel B shows the predicted performance of delayed broods under the Parent Quality hypothesis and Panel C shows the predicted performance of advanced broods under the Parent Quality hypothesis. 25**
- Figure 2.2: Pattern of reproductive performance predicted under the Date and Parent Quality hypotheses, on any given day during the season. Under the Parent Quality hypothesis, the magnitude of effects on performance should depend on the number of days the brood was either advanced or delayed.....26**

Figure 2.3. Mean nestling mass is positively associated with hatching difference late in the season (solid line and circles; $F=6.83$, $p=0.018$, $R^2=0.275$, $n=20$) but not early (broken line and squares; $F=0.245$, $p=0.627$, $R^2=0.015$, $n=18$). The early part of the season ranged from June 4 to 10. The late part of the season from June 11 to 20. 35

Figure 2.4. Female mass change is associated with the difference between actual and intended hatch date, but only in advanced broods ($F=7.86$, $p=0.017$, $R^2=0.417$, $n=13$). There is no relationship in delayed broods ($F=0.01$, $p=0.75$, $R^2=0.007$, $n=17$). There were 6 broods whose actual and intended hatch dates were exactly matched. Mass change is the difference in grams between incubation and provisioning in females. 36

Figure 3.1: Pattern of female mass change over the season in 1999 ($p<0.0001$, $F=24.93$, $R^2=0.416$, $n=37$). Mass change is the difference, in grams, between incubating (day 8) and provisioning (day 8) for each female..... 53

Figure 3.2: Female incubation mass (solid dots) declines significantly with lay date ($p<0.0001$, $F=21.46$, $R^2=0.333$, $n=45$) but provisioning mass (open dots) does not decline significantly with hatch date ($p=0.196$, $F=1.73$, $R^2=0.045$, $n=39$). 54

Figure 3.3: Female mass during provisioning (open dots) is negatively correlated with hatching difference ($p=0.004$, $F=9.21$, $r=0.204$, $n=38$) but incubation mass (solid dots) is not ($p=0.286$, $F=1.17$, $r=0.027$, $n=43$). 55

General Introduction

Seasonal declines in reproductive parameters are common among vertebrates and essentially ubiquitous in temperate breeding birds. Declines have been documented in offspring number (birds: Hochachka 1990, Winkler and Allen 1996, mammals: Huber *et al.* 1999, Kott and Robinson 1963, reptiles: Nussbaum 1981) offspring mass, growth or size (birds: Lepage *et al.* 1999, Sedinger and Flint 1991, mammals: Schultz and Johnson 1995, Fairbanks 1993, reptiles: James and Whitford 1994, Sinervo and Doughty 1996) or offspring survival (birds: Aparicio 1998, Norris 1993, Sanz 1999, mammals: Koskela 1998). The first comprehensive explanation for this phenomenon in birds (Perrins 1970) suggested that the timing of reproduction is dictated by the availability of food, as females may have to delay reproduction until resources are plentiful enough for them to gather sufficient energy for chick rearing. This theory has been refined over the years to incorporate variation in parent quality over the season, but, after three decades, the mechanism driving seasonal declines in reproductive performance remains unknown. A contributing factor is that little work has been experimental and without manipulating hatch date, it is not possible to determine whether aspects of date, such as food availability, determine seasonal declines in

reproductive success, or whether better quality parents breed early and subsequently produce more or better quality offspring.

Recently, hatch-date manipulation experiments have started to shed light on the proximate explanation for seasonal declines in reproductive success. These studies indicate that both timing *per se* and parent quality can drive seasonal declines in nestling performance both within and among species. In this thesis I present the results of a hatch-date manipulation experiment designed to test the predictions of two hypotheses for the seasonal decline in reproductive performance observed in Tree Swallows (*Tachycineta bicolor*).

Tree swallows are insectivorous passerines that nest in secondary cavities (Robertson *et al.* 1992). They arrive on breeding grounds all over North America in March or early April, and begin breeding in early May. Modal clutch sizes in this species range from 5 to 7. Females begin incubation on the day the penultimate or ultimate egg is laid and incubate for approximately 15 days. Nestlings remain in the nest for 19 to 22 days, after which they continue to be fed by parents for about a week (Robertson *et al.* 1992). Most nestlings hatch in early June.

Tree swallows exhibit seasonal declines in clutch size, nestling growth and nestling survival (Robertson *et al.* 1992, Stutchbury and Robertson 1988). They readily nest in artificial nest boxes and are amenable to handling and are therefore an ideal species for an

experimental investigation of the mechanism driving seasonal declines in reproductive performance.

The main focus of this thesis is to determine the proximate mechanism driving the seasonal decline in nestling mass in Tree Swallows. I manipulated hatch date by switching clutches differing in lay date, between nest boxes, thereby presenting parents with nestlings either earlier or later than they had anticipated. Two main hypotheses for the seasonal decline in nestling mass, the Date Hypothesis and Parent Quality Hypotheses, give mutually exclusive predictions about the reproductive performance of manipulated broods.

In Chapter 1 I demonstrate variation in parental response to an increase in brood demand and show how variation in provisioning behaviour impacts nestling quality just prior to nest departure. In Chapter 2 I describe the theory and predictions associated with both the Date and Parent Quality hypotheses, and present the results of the hatch-date manipulation experiment. Chapter 3 is an examination of possible biases that might complicate interpretation of hatch-date manipulation experiments, such as heritability, maternal effects or unintentional impacts of the experiment on parent quality. Chapter 4 is a literature review of studies that have manipulated hatch date, and an assessment of the conclusions drawn from these studies. I integrate the results of the research presented in this thesis with the findings of

hatch-date manipulation experiments in other species. I finish with a brief general discussion of the ideas presented in this thesis.

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Chapter 1

Variation in provisioning ability of parent Tree Swallows

Introduction

Individual variation in parent quality is thought to impact avian reproductive success. For example, it is known that younger, less experienced birds often lay smaller clutches and exhibit lower seasonal reproductive success than more experienced individuals (e.g. Hipfner *et al.* 1997, Stutchbury and Robertson 1988). I define parent quality as an inherent characteristic of individuals that is determined by the sum of the morphological and physiological characteristics that determine parents ability to rear their young. Examples of these characteristics include age, immunological health and current energy reserves. Typically parent quality is defined in terms of an individual's relative performance in some reproductive parameter. Reproductive parameters that are often assessed include lay date, fledging success, probability of nestling recruitment, egg size or nestling growth. There is not a universal definition of parent quality available in the literature. Provisioning ability is one of the most critical aspects of parental care as nestling body mass is directly related to the amount of food provisioned, and nestling mass is known to correlate with survival to independence in many passerine species (e.g. Macgrath 1991, Hochachka and Smith

1991, Smith *et al* 1989). The purpose of this study was to establish the existence of variation in provisioning ability among parent Tree Swallows, and to determine whether this variation is correlated with nestling mass just prior to nest departure.

To address this question demand was manipulated in a nestbox population of Tree Swallows by increasing brood size for 48 hours and assessing the parental response to that increased demand by measuring chick growth. Higher growth would show that parents are more capable of increasing effort in response to demand, or are willing to expend extra resources for their current reproductive effort. Parents were then 'reset' by replacing all nestlings in the nest with new, previously unmanipulated, nestlings to independently determine whether those parents that performed best during the provisioning test also produce higher quality nestlings. If so, this indicates either that reproductive performance is a consequence of individual variation in parental ability to provision, or that some parents are more willing to increase effort in response to demand during the current reproductive attempt.

Methods

Study area and breeding phenology

This study was carried out during May and June of 1998, on the Creston Valley Wildlife Management Area, a managed wetland in south-

eastern British Columbia, Canada (49° 05' N and 116° 35' W). Two hundred Tree Swallow nestboxes mounted on stakes are spaced approximately 15 - 30 m apart along dykes surrounding a series of ponds. Nests were checked daily beginning May 1 until the end of the season. Lay date of each egg, clutch completion date and hatch date were recorded. Hatch date was assigned as the first day on which half or more of the eggs in a clutch had hatched, and was considered day 1 of the nestling period. Date is presented as days from May 1 (May 1= 1, June 1= 32).

Parental Provisioning Response

In order to assess provisioning response (PR), I challenged parents by adding extra nestlings to their brood for a period of 48h, and measured the growth of nestlings over this period. I assumed that nestlings that grew faster were better provisioned. On day four of the nestling period, broods were increased to 8 nestlings, regardless of initial brood size, using additional nestlings from donor nests not included in the study. Nestlings were individually marked with pieces of coloured opaque plastic tubing and weighed to the nearest 0.01g on a portable pan balance. All measurements were taken before 0800h. Nestlings were reweighed 48h later, and the increase in mass of the whole brood over this period (gh^{-1}), is my measure of parental provisioning response

(PR). After the second measurement, all broods were returned to their original brood size of either five or six nestlings and all nestlings used in the PR test were removed from the nest and replaced with new, previously unmanipulated nestlings, which were weighed at this time.

Nestling characteristics

Nestlings were reweighed and measured on day 15 of the nestling period. Mass was recorded to the nearest 0.01g using a digital pan-balance. Tarsus, bill length, bill width, bill depth and length of the right 9th primary feather (from the insertion point to the tip of the unflattened feather) were measured with metal vernier calipers to 0.02mm. Head-bill length, from the tip of the bill to the furthest point at the back of the head, was measured with plastic dial calipers to the nearest 0.05mm. Wing span was measured as twice the distance from the center of the feather tract along the back, to the tip of the outstretched wing. Body length was measured to within 1mm, from the tip of the bill to the tip of the longest rectrix feather, using a metal ruler. Structural size was the first principal component score of a principal component analysis of all nestling measurements, excluding mass. All nestling measurements are presented as brood means. All analyses were done using JMPIN 3.2.1 (SAS Institute 1997). Relationships were considered statistically significant at $p < 0.05$. The effects of brood size, date and PR on nestling

mass and size was assessed using multiple regression, as was the relationship between PR and date. All tests are 2-tailed.

Results

Parents with a higher provisioning response (PR) produced nestlings that weighed more at day 15 than those with lower PR (Figure 1.1a). Nestlings in broods of five were also larger at day 15, on average, than those reared in broods of six (mean mass for brood of 5 = 22.87 ± 1.44 (SD), 6 = 21.32 ± 1.58 (SD); $F = 6.15$, $p = 0.025$, $n = 18$). Parents with high PR produced structurally larger nestlings (Figure 1.1b), though there was no difference in structural size between nestlings reared in broods of five or six (mean PC1 for broods of 5 = 0.48 ± 0.89 (SD), 6 = 0.18 ± 1.23 (SD); $F = 0.64$, $p = 0.44$, $n = 18$). Neither nestling mass nor nestling structural size declined significantly over the season, though there was a very strong decline in PR (Figure 1.2). There was no effect of initial brood size on PR ($t = -0.256$, $p = 0.80$, $n = 18$). There was also no correlation between mass of day six nestlings at the end of the PR test, and the mass of replacement nestlings at day six ($r = -0.39$, $p = 0.10$, $n = 18$). If anything, there was a tendency for parents with high PR to be given smaller replacement nestlings.

Figure 1.1. (a) Residuals of mean nestling mass (NM) on brood size and (b) mean structural size (PC1), are positively correlated with provisioning response (PR) (NM - $F = 5.19$, $p = 0.038$, $n=18$, $r=0.511$; PC1 - $F = 6.69$, $p = 0.02$, $n = 18$, $r = 0.501$). The regression equation for the lines are $NM = - 9.13 + 11.90 PR$. and $PC 1 = -6.84 + 9.30 PR$.

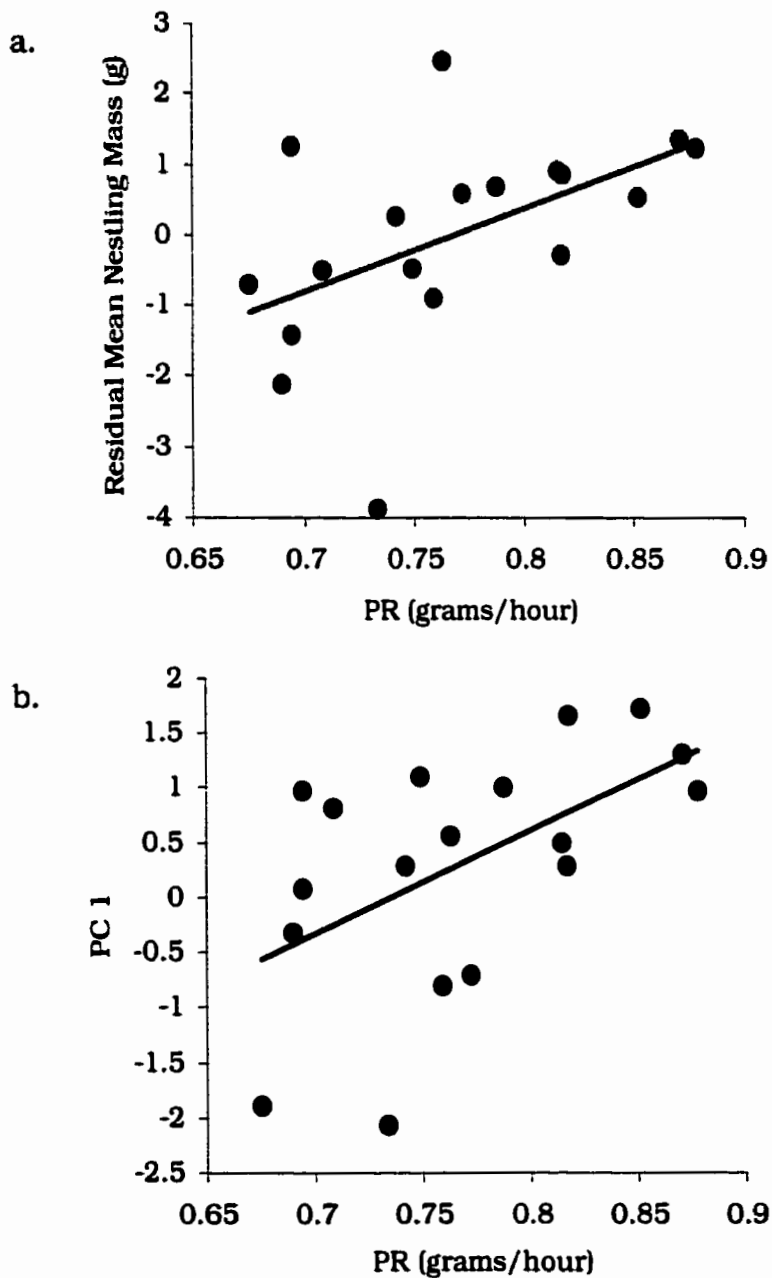
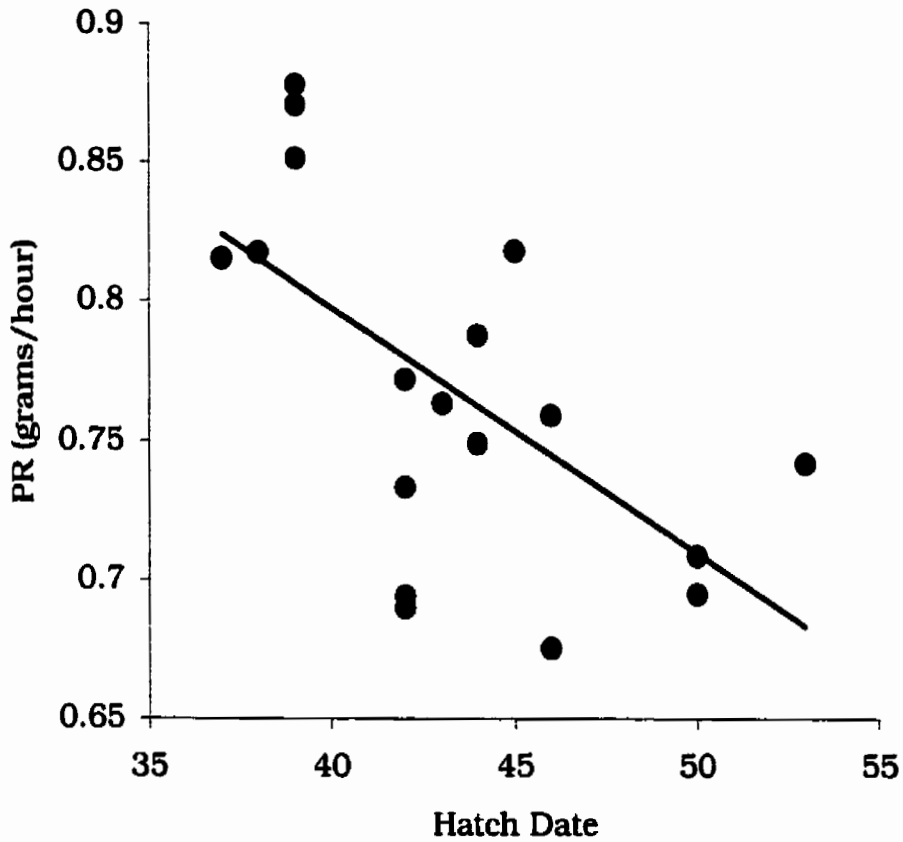


Figure 1.2: PR, measured as change in total brood mass/hour, declines with hatch date ($F = 9.41$, $p = 0.007$, $n = 18$, $r^2 = 0.331$). The equation for the line is $PR = 1.149 - 0.009 \text{ Hatch Date}$.



Discussion

The results of this study demonstrate that parents with a high provisioning response produce nestlings that are both heavy and structurally large. Since parents are not related to the nestlings they rear after day six, these correlations are not attributable to maternal effects or heritability. There was also no correlation between day six mass of the chicks used in the PR test and the day six mass of replacement chicks. If anything, parents performing best during the PR test were given the smallest chicks, further reducing the likelihood of detecting an effect of PR on nestling quality.

Since PR strongly impacted nestling mass and size, and PR declined over the season, it is surprising that nestling mass and size were not correlated with hatch date. Though there was a trend for nestling mass to decline over the season, this trend was not significant (slope = - 0.01 g/d, $F=1.00$, $p=0.33$). This could be because, once the notable effect of PR on nestling mass and size had been accounted for, there was little additional influence of date. In addition, I would not expect the slope of the decline in nestling mass to be as great as that in PR for two reasons. First, in the PR test, demand was increased which should have magnified the extent of the differences in provisioning response, while variation in nestling mass and size was determined

under normal brood sizes. Secondly, at day 6 parents were 'reset' with new nestlings, reducing the amount of time available for individual differences in provisioning to be manifested as differences in nestling mass. In addition, since there was a tendency for parents with high PR to receive smaller replacement nestlings additional effects of date may have been difficult to detect, as any natural seasonal trends were unintentionally reversed.

Nestlings reared in broods of five were, on average, larger than those reared in broods of six. This is likely because there is a greater amount of food provisioned per offspring, a phenomenon that has been demonstrated in other species (Smith *et al* 1989, Kunz and Ekman 2000, Sanz and Tinbergen 1999). Though there was not a detectable difference in nestling size, measured as PC1, between five and six chick broods, there was a positive correlation between PR and PC1, meaning that parents which responded best to the provisioning test, also reared structurally larger nestlings. These results indicate that a large component of nestling quality, measured as nestling mass and size, is attributable to individual variation in parental provisioning.

There was no evidence that PR was influenced by initial brood size, suggesting that clutch size is not a good predictor of the number of nestlings parents are able to provision. This has been demonstrated previously in Great Tits (Both *et al* 1998), in which a cross-fostering

experiment demonstrated that initial clutch size does not predict performance in manipulated broods. If PR is an inherent characteristic of parents ability to provision young, it is not reflected in their choice of offspring number.

PR declined significantly over the season. If this measurement reflects individual variation in parent quality, as opposed to a greater willingness of early breeders to expend energy in reproduction, this means that higher quality parents are breeding early in the season. This could help explain the observed seasonal decline in reproductive performance known in so many avian species (Hochachka and Smith 1990, Sedinger and Flint 1991). It is possible, however, that early in the season, aspects of date *per se*, caused the observed seasonal decline in PR. If, for example, food availability declined systematically over the season, and impacted all provisioners equally, then it may have been easier for early parents to collect food to provision to offspring, and thus perform better during the PR test. Likewise, if the value of later hatched young is reduced, later breeders may just be choosing not to respond to the increase in demand due to the reduced benefits of reproductive investment. If this were the case, performance would be linked to date *per se*, because the value of young on a given date would determine how much parents responded to the change in demand. The only way to distinguish whether higher quality parents are in fact breeding earlier in

the season is to experimentally manipulate reproductive timing. In Chapter 2 I will present the results of a hatch-date manipulation experiment designed to distinguish whether date or parent quality determines the seasonal decline in reproductive performance in Tree Swallows.

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Chapter 2

Seasonal declines in reproductive performance: testing the date and parent quality hypotheses

Introduction

Seasonal declines in reproductive performance have been observed in a wide variety of avian taxa. These declines result from a reduction, in the population over the course of the season, in fitness-related parameters such as nestling mass and growth (Hochachka 1990, Sedinger and Flint 1991), clutch size (Winkler and Allen 1996); nestling survival (Norris 1993, Wiggins *et al.* 1994) and nestling recruitment (Hochachka and Smith 1991). Although the occurrence of these declines is well established, the underlying mechanisms remain unclear. The purpose of this study is to determine the proximate mechanism driving seasonal declines in nestling characteristics of Tree Swallows.

Two main hypotheses have been proposed to explain seasonal declines in reproductive performance: the Date and Parent Quality hypotheses. The Date hypothesis states that seasonal declines in reproductive variables are due to systematic deterioration of some aspect of the environment over the season that impacts all individuals equally. Reproductive performance is therefore dependent on the date of clutch

initiation. Characteristics associated with date that could influence seasonal reproductive success (SRS) include a reduction of the food supply, an increase in the level of competition among juvenile conspecifics (Nilsson 1999) or an increase in predation risk over the season.

The Parent Quality hypothesis states that parents initiate clutches on the date that maximises their lifetime reproductive success (LRS), given the amount of energy they currently have available for reproduction. Parent quality could be determined by parental age, provisioning ability or territory quality, but are generally characters that are inherent to the individual. If a seasonal decline in condition causes the observed decline in nestling characteristics, performance will be independent of date. The only way to distinguish between the Date and Parent Quality hypotheses is to manipulate reproductive timing.

The Parent Quality hypothesis is not quite the same as the Individual Optimisation Hypothesis often applied to studies of the causes of clutch size variation. Clutch size might be optimised at the number of eggs that will maximise offspring production, given an individual's current condition. Any adjustment to the optimal clutch size would result in a reduction in fitness. In timing experiments, it is more appropriate to view birds as being driven to breed as early as possible, with the first possible breeding date determined by the individual's

current condition, thus the alternative to the Date hypothesis in this experiment will be the Parent Quality hypothesis, as opposed to Individual Optimisation.

Previous studies have manipulated reproductive timing in a variety of ways: delaying hatch date by replacing clutches with dummy eggs for a portion of the incubation period (Morbey and Ydenberg 2000, Wiggins *et al.* 1994); by forcing replacement clutches through removal of first clutches (Verhulst and Tinbergen 1991, Verhulst *et al.* 1995); or manipulating hatch date by switching clutches with differing lay dates (Aparicio 1998, Brinkhof 1995). In this study I moved clutches between nests to alter hatching dates.

The Date and Parent Quality hypotheses yield mutually exclusive predictions about the outcome of experiments that manipulate hatch date. These predictions are illustrated graphically in Figure 2.1. The Date hypothesis predicts that the performance of clutches manipulated to hatch earlier or later than parents had expected will match that of unmanipulated parents broods hatching on the same day. This is because characteristics explicitly related to hatch date drive seasonal declines in performance. The Parent Quality hypothesis predicts that performance of parents with manipulated nestling hatch dates will match that of unmanipulated parents whose nestlings hatch date coincides with the original hatch date. Performance of delayed parents on their brood's

manipulated hatch date will be high, relative to that of unmanipulated broods hatching on the same day, because performance of delayed parents is matched to their nestling's earlier, intended hatch date. Generally, delayed parents should perform better than unmanipulated or advanced parents. Performance of advanced parents, over the season, will be lower than that of unmanipulated or delayed parents. Figure 2.2 illustrates the predicted pattern of reproductive performance in relation to the magnitude of the difference between actual and intended hatch date under both the Date and Parent Quality hypotheses.

In this chapter I look at the effects of the hatch-date manipulation experiment on nestling characteristics that might be associated with fitness.

Figure 2.1. Expected outcome of hatch-date manipulation experiments under the Date and Parent Quality hypotheses. Solid lines represent the natural seasonal trend, arrows indicate the direction of manipulation and the shaded area represents the predicted performance of manipulated broods. Panel A shows the predicted performance of manipulated broods under the Date hypothesis. Panel B shows the predicted performance of delayed broods under the Parent Quality hypothesis and Panel C shows the predicted performance of advanced broods under the Parent Quality hypothesis.

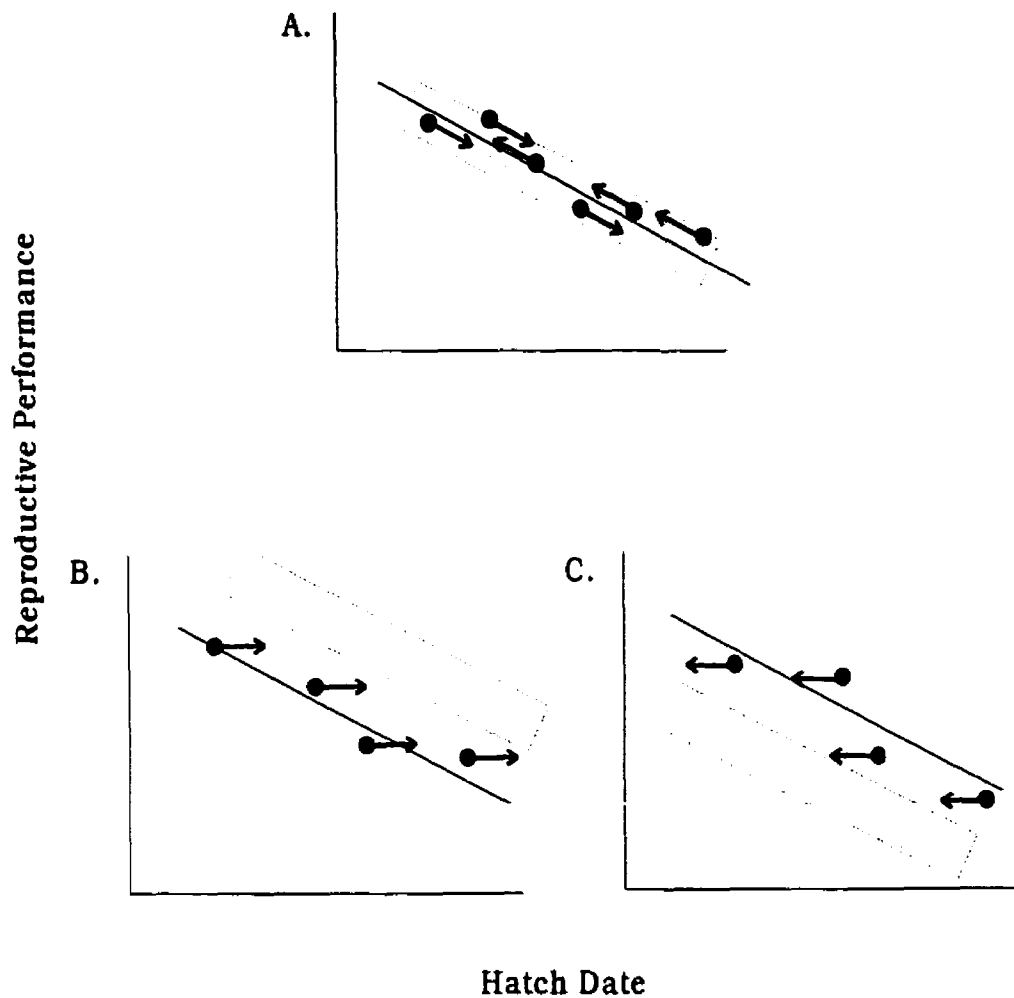
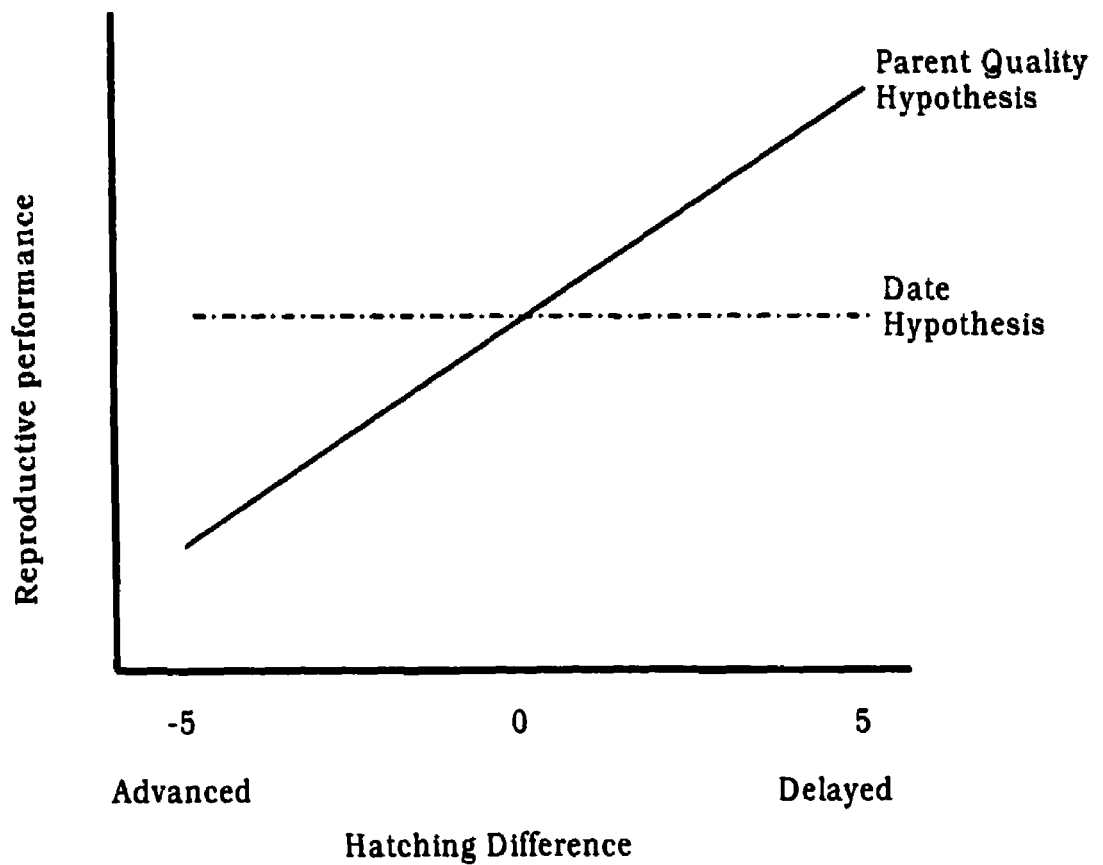


Figure 2.2: Pattern of reproductive performance predicted under the Date and Parent Quality hypotheses, on any given day during the season. Under the Parent Quality hypothesis, the magnitude of effects on performance should depend on the number of days the brood was either advanced or delayed.



Methods

Study area and breeding phenology

This study was carried out during May and June of 1999, on the Creston Valley Wildlife Management Area, a managed wetland in south-eastern British Columbia, Canada (49° 05' N and 116° 35' W). Two hundred Tree Swallow nestboxes mounted on stakes are spaced approximately 15 - 30 m apart along dykes surrounding a series of ponds. Nests were checked daily beginning May 1 until the end of the season. Lay date of each egg, clutch completion date, hatch date and incubation date were recorded. Hatch date was assigned as the first day on which half or more of the eggs in a clutch had hatched, and was considered day 1 of the nestling period. Onset of incubation was typically easy to detect by feeling egg temperature, but was occasionally ambiguous. In these cases the date the last egg was laid was considered the first day of incubation, as 79% of all broods with known incubation timing, initiated incubation on the last egg. Date is presented as days from May 1 (May 1= 1, June 1= 32). Eggs were numbered in laying sequence using a black, non-toxic, waterproof marker. The first 120 eggs laid were weighed using a portable pan balance to the nearest 0.01g, and maximum length and breadth of all eggs was measured with metal

calipers to the nearest 0.02mm. Mass of all eggs was estimated from length and breadth using equations in Hoyt (1979).

Experimental Protocol

Hatch date was manipulated by switching clutches differing in onset of incubation. Clutches at day 6 of incubation were paired with those at day 10, and switched. As a result, those parents whose eggs had been incubated for 6 days, were incubating eggs that had been developing for 10 days, and would therefore hatch 4 days earlier than expected. These will be referred to as 'advanced' broods. Parents that had been incubating for 10 days, received eggs that had been developing for only 6 days and would therefore hatch 4 days later than expected. These will be referred to as 'delayed' broods. Broods at the same incubation timing were switched at day 10 to serve as controls. A manipulation of 4 days represents a significant adjustment to an individual's relative reproductive timing, as hatch dates in the entire population varied by only 16 days. Due to error associated with estimating incubation timing, the actual magnitude of the manipulation was variable with broods advanced or delayed by as much as 5 days, and including broods matched equally in timing. This measure will be referred to as Hatching Difference, and was calculated as the hatch date of the brood in the nest minus the hatch date of the parents' actual brood.

in the foster nest. In all, 47 clutches were manipulated. Of those, one clutch did not hatch and eight died before day 15 leaving a sample of 38 nests that survived to the end of the study. Females in their first year can be distinguished by their brown plumage (Stutchbury and Robertson 1988), and were excluded from the study to avoid possible confounds of age.

Eggs were moved quickly, and transported in small plastic containers nestled in cotton balls and heated with "Hot Pocket" air activated handwarmers. All clutches were adjusted to six eggs, and at hatching adjusted again if necessary to six with nestlings from broods elsewhere on the study site.

Parental Characteristics

Both parents were captured on the nest. Females were captured at day 8 of incubation, and weighed to the nearest 0.5g with a Pesola spring balance. This is termed 'incubation mass'. Female tarsus length was measured to the nearest 0.02mm with metal vernier calipers. Tarsus length serves as a measure of structural size. Females were captured and weighed a second time on day 8 of chick rearing. This is termed 'provisioning mass'.

Males were captured on day 8 of chick rearing and weighed and measured in the manner for females described above. Both genders were

marked with numbered, metal leg bands. One female of 47 was not captured at either time. Approximately half of the males (24) were captured.

Nestling mass

Chicks were weighed and measured on day 15 of the nestling period. The mean mass of the entire brood was used as the performance measure. Chicks were weighed to the nearest 0.01g using a portable electronic balance. Mean nestling mass has been shown to reflect survival to independence in many species (e.g. Macgrath 1991).

Statistical Analysis

Because broods were not advanced or delayed by exactly 4 days, but ranged from advances of 5 days to delays of 5 days, I used the difference between the true and intended hatching date as a measure of my experimental manipulation. I treated this measurement as a continuous variable referred to as 'hatching difference'. Nests were grouped in advanced (-5 to -2 d), control (-1 to 1d) and delayed (2 to 5d) to assess whether there was any bias in the random assignment of nests to treatment.

In order to test whether hatching difference had any effect on brood mass, a backward stepwise multiple regression procedure was used. All variables with at p-value of less than the 0.1 were included in

the final model. Correlation coefficients were calculated using a partial correlation analysis. All analyses were done using JMPIN 3.2.1 (SAS Institute Software, 1997).

Results

Characteristics of Treatment Groups

There was no apparent bias in the assignment of broods to treatment groups. Original clutch size, male and female tarsus length and egg mass did not differ among treatment groups (Table 2.1).

Hatching Difference

The results of the multiple regression analysis investigating the impact of hatching date and difference on mean nestling mass are presented in Table 2.2. Hatching difference has a significant and positive effect on brood mass, when hatch date is held constant. The effects on mean nestling mass are, however, complicated by a highly significant interaction between treatment and hatch date, shown in Fig 2.3. To assess the nature of this interaction, the season was split into two portions, early and late, on the day that split the sample as close as possible into half. Early in the season, there is no effect of the manipulation on nestling mass, which is consistent with the Date hypothesis (compare with Figure 2.2). In the second half of the season,

there is a positive effect of hatching difference on nestling mass, which is consistent with the Parent Quality hypothesis (compare with Figure 2.2).

Impacts of the Experiment on Parent Quality

To discriminate between the Date and Parent Quality Hypotheses, hatch-date manipulation experiments require that parent quality is not affected by the manipulation. Tree Swallow females lose mass as the incubation period progresses and my manipulation apparently affected the amount of mass females lost during the late incubation and early brood rearing periods. Females lost mass from incubation (measured on day 8) to chick rearing (measured on day 8; Figure 2.4). Mass loss in advanced females was directly related to the number of days they were advanced, but there was no effect of the treatment on control or delayed females (Fig. 2.4). If female mass loss somehow contributes to parent quality, then advanced parents cannot be evaluated in the same way as control and delayed. I discuss the potential impacts of female mass loss on reproductive performance in Chapter 3.

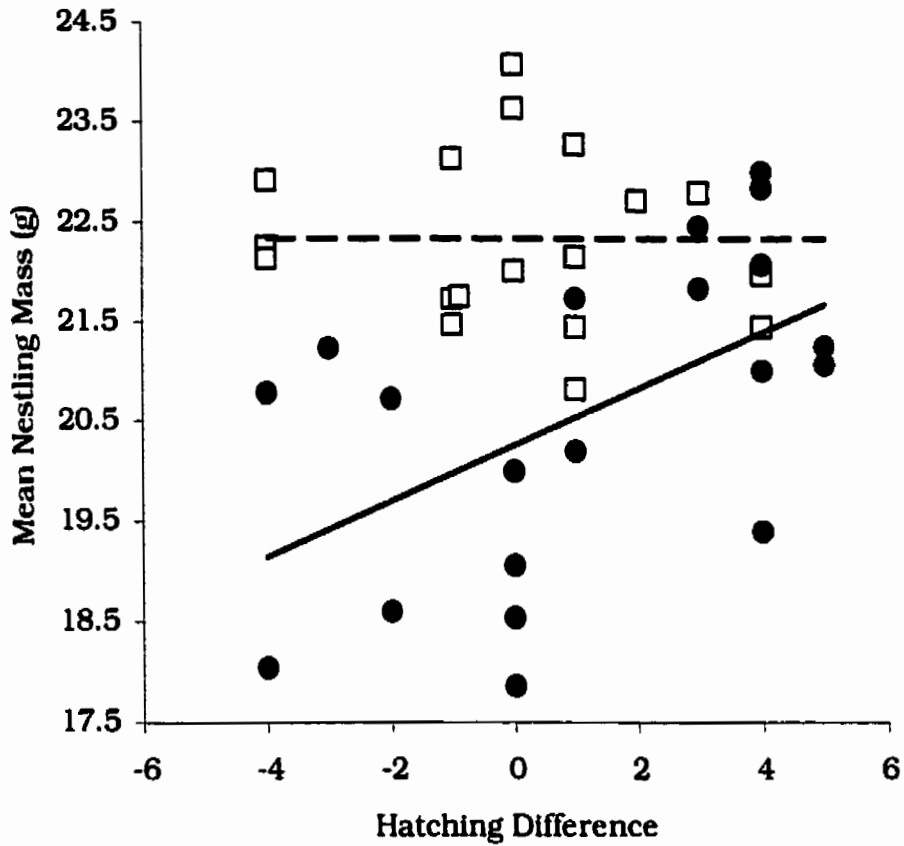
Table 2.1. Characteristics of the 3 treatment groups. There is no statistical evidence of treatment differences in any of these variables. All variables were compared using ANOVA. Parameters are those of foster parents. Sample sizes are in parentheses. a = advanced, c = control, d = delayed.

Parameter	Mean Values	df	F	p
Clutch Size (47)	a - 5.71 (14) c - 5.95 (20) d - 6.00 (13)	2	0.73	0.49
Female Tarsus (46)	a - 12.22 (13) c - 12.38 (20) d - 12.13 (13)	2	2.00	0.15
Male Tarsus (24)	a - 12.00 (7) c - 12.06 (10) d - 12.13 (8)	2	0.39	0.68
Egg Mass (47)	a - 1.84 (14) c - 1.84 (20) d - 1.89 (13)	2	0.61	0.54

Table 2.2. Multiple regression analysis of the variation in mean nestling mass. $R^2=0.297$, $n=38$. Hatching difference was not known for one brood. Correlation coefficients (r) were calculated using partial correlation analysis including mean nestling mass, hatch date and treatment.

Source	df	F	p	r
Hatch Date	1	16.30	0.0003	-0.42
Hatching Difference	1	6.98	0.0120	0.33
Hatch Date * Hatching Difference	1	7.95	0.0008	--

Figure 2.3. Mean nestling mass is positively associated with hatching difference late in the season (solid line and circles; $F=6.83$, $p=0.018$, $R^2=0.275$, $n=20$) but not early (broken line and squares; $F=0.245$, $p=0.627$, $R^2=0.015$, $n=18$). The early part of the season ranged from June 4 to 10. The late part of the season from June 11 to 20.



Discussion

My results show that mean nestling mass declined significantly over the season and responded to the hatch-date manipulation differently at different points in the season. Early in the season, mean mass of nestlings was apparently uninfluenced by the manipulation, a response predicted by the Date hypothesis. Late in the season, however, delayed nestlings were heavier, as predicted by the Parent Quality hypothesis.

A number of previous studies have generated evidence that lower quality parents reproduce later in the season (Aparicio 1998, Brinkhof 1995, Brouwer *et al.* 1995, De Forest and Gaston 1996, Hipfner 1997, Hipfner *et al.* 1999, Morbey and Ydenberg 2000) but many studies find support for the Date hypothesis (Hedgren and Linnman 1979, Lepage *et al.* 1999, Moreno *et al.* 1997, Norris 1993, Sanz 1999, Verboven and Visser 1998, Verhulst *et al.* 1995). Several studies have found support for both hypotheses in a single species (e.g. Brinkhof 1995, Verhulst and Tinbergen 1991, Verhulst *et al.* 1995, Wiggins *et al.* 1994). The presence of an interaction between date and treatment in the multiple regression analysis of mean nestling mass in this study also demonstrates the presence of both mechanisms within a single species. There are a variety of explanations for this disparity in results. It may be that different mechanisms act in different species. While it is unlikely that species can

be separated into those whose SRS is dictated by date and those dictated by parent quality, it is possible, that there is a dominant mechanism, and that the dominant mechanism differs among species.

Another possibility is that the mechanism responsible for variation in SRS differs from year to year. In some years parent quality may strongly influence reproductive performance, while in other years, any effect of parent quality is overridden by environmental conditions such as food availability. The few long term studies that attempt to discern the mechanism driving seasonal declines find annual variability in the dominant mechanism (Brinkhof 1995, Verhulst *et al.* 1995). The result of single year studies may depend predominantly on the environmental conditions in the year it was conducted. In fact, this idea might help explain the apparent difference in mechanisms operating early vs. late in the season, as found in this study and in others (e.g. Brinkhof 1995). If, for example, food abundance is low early in the year, the availability of food may override the influence of parent quality on nestling characteristics. A hatch-date manipulation experiment by Verhulst and Tinbergen (1991) found separate support for the Date and Parent Quality hypotheses in two forests in the Netherlands, and attribute this to the measurable difference in food abundance in the two forests. If food abundance declined over the season this could explain the discrepancy in results.

An additional factor that has never been fully addressed in studies that manipulate hatch date is the possibility that the manipulation itself alters parent quality. If relaying a clutch or incubation is costly, the results of studies inducing clutch replacement or altering incubation would be biased towards the Date hypothesis, because delayed parents pay an extra, unanticipated cost and might perform more poorly than expected for their chosen hatch date. Advanced parents would perform better than expected as they pay less cost than they would have under natural conditions. The effect would mimic a seasonal decline. In some years it might be possible to detect parent quality effects in spite of these manipulations, but in poor years or in studies with low power, it might not be possible to discern effects of date from effects of the manipulation itself.

In conclusion, parent quality seems to drive the seasonal decline in reproductive performance in Tree Swallows, but this effect is either absent or not detectable early in the season. There is evidence that the experimental manipulation altered parent quality, at least in advanced broods. The importance of female mass loss in interpreting the results of this experiment is discussed in Chapter 3.

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Chapter 3

Sources of bias in hatch-date manipulation experiments

Introduction

Experimental manipulations of hatch date are necessary to distinguish between the effects of date and parent quality on reproductive performance. Although hypotheses make clear predictions about the outcome, interpreting hatch-date manipulation experiments may be complicated by biases towards support for the Date hypothesis. Such biases include heritability of, or maternal effects on, the performance measure in question and unintentional manipulation of parent quality. Therefore, whenever a hatch-date manipulation experiment finds support for the Date hypothesis, it is necessary to address whether these biases are present. In this chapter I ask whether potential biases affected the outcomes presented in Chapter 2.

The predictions of hatch-date manipulation experiments are based on the assumption that the link between parent quality and performance is behavioural, and that 'high quality' parents perform well because they are better able to provision offspring. If the link between parent quality and nestling performance occurs via genetic or maternal effects, the same predictions can not be made because nestling performance would be partly determined before foster parents ever provision offspring. A

recent review of what is known about the cause of seasonal declines in avian reproductive success (Nilsson 1999) refers to heritability and maternal effects as a separate hypothesis, called the 'Chick Quality hypothesis', in which performance is determined in the chick, prior to hatching. Nilsson does not present any studies that assess this hypothesis and previous studies have rarely addressed the possible contribution of heritability and maternal effects to nestling performance in the context of a hatch-date manipulation experiment.

It is not possible to distinguish additive genetic variance from maternal effects without cross-fostering offspring, a design in which each parent raises some of its own offspring and some foster offspring. Typically, however, characteristics such as offspring size are largely determined by additive genetic variation (e.g. Smith and Wettermark 1995 $h^2=0.43$, Wiggins 1989 $h^2=0.50$) while effects of egg size are generally maternal effects (Bernardo 1996b).

There is evidence of heritability both in life history traits and morphology in birds. Schluter and Gustaffson (1993) demonstrated heritability in clutch size and laying date in the Collared Flycatcher (*Ficedula albicollis*). Many studies have demonstrated heritability of body size in birds (Tree Swallow, Wiggins 1989, Pied Flycatcher (*Ficedula hypoleuca*), Alatalo and Lundberg 1986, European Starling (*Sturnus vulgaris*), Smith and Wettermark 1995, but see Kunz and Ekman 2000).

If high quality parents breed earlier in the season, production of higher quality offspring may be due to heritability of aspects of reproductive performance, measured as nestling mass or size. In this case, hatch-date manipulations will always support the Date hypothesis because performance will match that of the actual parents' hatch date, and therefore follow the seasonal trend. In this chapter I use correlations between actual mother and offspring tarsus lengths to assess heritability of body size in Tree Swallows in an attempt to determine whether there is evidence of heritability in some aspect of nestling morphology. The only way to properly assess whether heritability may cause bias in this experiment would be to assess heritability of nestling body mass. Unfortunately, the mass of parents when they were nestlings was unknown, so this was not possible. Assessing heritability in nestling size will not lead to the conclusion that heritability is a source of bias in this experiment, but if present, will illustrate the potential for such problems to arise.

Maternal effects are defined as the direct effect of a parent's phenotype on the phenotype of its offspring (Bernardo 1996a). They influence offspring phenotype over and above the direct effects of the offspring's genes or nest environment. For instance, passive transfer of antibodies from mother to offspring via the egg is a maternal effect that could influence nestling performance (Burley and Vadehra 1989). Egg

size and quality are often considered maternal effects (Bernardo 1996b) as things like nutrients and antibodies transferred via the egg can confer advantages to the resulting nestlings. If this is the case, hatch-date manipulations will be biased towards supporting the Date hypothesis because any advantages are conferred by the actual mother, and therefore performance will match the hatch date intended by the actual parents. In this chapter I look for correlations between egg mass and nestling performance to address whether maternal effects could be causing bias in the interpretation of my hatch-date manipulation experiment presented in Chapter 2.

Finally, experiments that manipulate hatch date assume that the manipulation itself does not alter parent quality. If parent quality is altered by a hatch-date manipulation, then results will be biased towards the Date hypothesis. This is because delaying hatch date results in increased costs to parents via increased incubation periods (in the case of clutch switching experiments) or extra energy expended to produce a second clutch (in the case of induced relaying experiments). Advanced parents would pay a reduced cost in clutch switching experiments via decreased incubation periods. The end result would be that advanced parents perform better than expected under the Parent Quality hypothesis, and delayed parents perform more poorly than expected, causing performance to approximate the natural seasonal trend. If costs

imposed by the manipulation are significant and statistical power is low, hatch-date manipulation experiments that impact parent quality would not support the Parent Quality hypothesis, even in the presence of a seasonal decline in parent quality. In chapter 2 I presented evidence that my manipulation influenced the amount of mass females lost over the reproductive cycle. It is possible that mass loss is associated with parent quality and if so, this could have resulted in a reduction in my ability to detect parent quality effects. In this chapter I will discuss the possibility that my experiment altered parent quality via mass loss and its significance in interpreting my hatch-date manipulation experiment.

Methods

This study was carried out during May and June of 1999, on the Creston Valley Wildlife Management Area, a managed wetland in south-eastern British Columbia, Canada (49° 05' N and 116° 35' W). Refer to Chapter 2 for a detailed description of the basic methods, used to measure and mark Tree Swallows.

Heritability

Heritability of tarsus length was assessed as the correlation between the length of mother's tarsus with that of her offspring. Tarsus length of male parents was not considered due to the small number of males captured relative to the number of females (24 vs 46) and the high

rate of extra-pair copulations in this species, making paternity uncertain (Robertson et al. 1992). Egg dumping is infrequent in this species (Robertson et al. 1992), and I can therefore be fairly confident in assigning maternity. The slope of the regression of mother versus offspring tarsus is equivalent to $\frac{1}{2}h^2$ (Falconer and Mackay, 1996), with h^2 representing the heritable component of the trait. Heritability was therefore quantified by doubling the slope of the correlation between offspring and mother's tarsus.

Statistical Analysis

See Chapter 2 for a description of the experimental treatment variable. I used a backwards stepwise multiple regression procedure to investigate how variables correlated with my nestling measurements. All variables with $p < 0.10$ were included in the final model. Correlation coefficients were calculated using a partial correlation analysis. All analyses were done using JMPIN 3.2.1 (SAS Institute Software, 1997).

Results

Heritability and Maternal Effects

Tarsus

Mean nestling tarsus length at day 15 was positively correlated with mother's tarsus length but not with female foster parent tarsus length (Table 3.1). Tarsus length has a heritable component in this population estimated as $h^2=0.56$.

Egg Mass

I looked for correlations between egg mass and nestling mass at days 4 and 15, and nestling tarsus length at day 15. There was no relationship between egg mass and nestling mass or tarsus length at day 15 but there was a positive correlation between nestling mass at day 4 and egg mass (Table 3.1).. This indicates that the influence of egg mass on nestling characteristics was transitory and most important early in the nestling period. Nestling mass at day 4 did not decline over the season ($p=0.55$, $F=0.363$, $r=0.09$, $n=47$), while egg mass increased over the season ($p=0.008$, $F=7.404$, $r=0.288$, $n=84$).

Female Mass Loss

Females lost mass between day 8 of incubation and day 8 of chick rearing. The amount of mass lost declined significantly over the season (Figure 3.1). The decline was due to a decline during incubation and not provisioning mass which did not decline over the season (Figure 3.2). Female mass loss was also significantly correlated with the duration of the incubation period (see Chapter 2). Note that the relationship between hatching difference and mass loss arose because advanced females had higher masses during provisioning (Figure 3.3).

Table 3.1: Backwards stepwise regression analysis of the variation in nestling mass at day 15 (M15), tarsus length at day 15 (TL) and nestling mass at day 4 (M4). Means were averages of broods. Non-significant variables ($p < 0.10$) were dropped from the model. Model adjusted $R^2 = 0.297$ (M15), 0.288 (TL) and 0.313 (M4). Correlation coefficients were calculated using a partial correlation analysis. Where F is blank, the variable was dropped from the analysis because $p > 0.10$.

Source	df	Mean day 15 nestling mass per brood (g), n=38			Mean day 15 tarsus length per brood (mm), n=38			Mean day 4 nestling mass per brood (g), n=47		
		F	P	r	F	P	r	F	P	r
Hatch Date	1	16.30	0.0003	-0.42	11.71	0.002	0.50			ns
Hatching Difference	1	6.98	0.012	0.33		ns				ns
Hatch Date * Hatching Diff.	1	7.95	0.0008			ns				ns
Mother Tarsus	1		ns		6.26	0.017	0.39			ns
Foster Mother's Tarsus	1		ns			ns				ns
Egg Mass	1		ns			ns		4.87	0.030	0.31
Foster Mother's Mass Loss	1		ns			ns				ns

Figure 3.1: Pattern of female mass change over the season in 1999 ($p < 0.0001$, $F = 24.93$, $R^2 = 0.416$, $n = 37$). Mass change is the difference, in grams, between incubating (day 8) and provisioning (day 8) for each female.

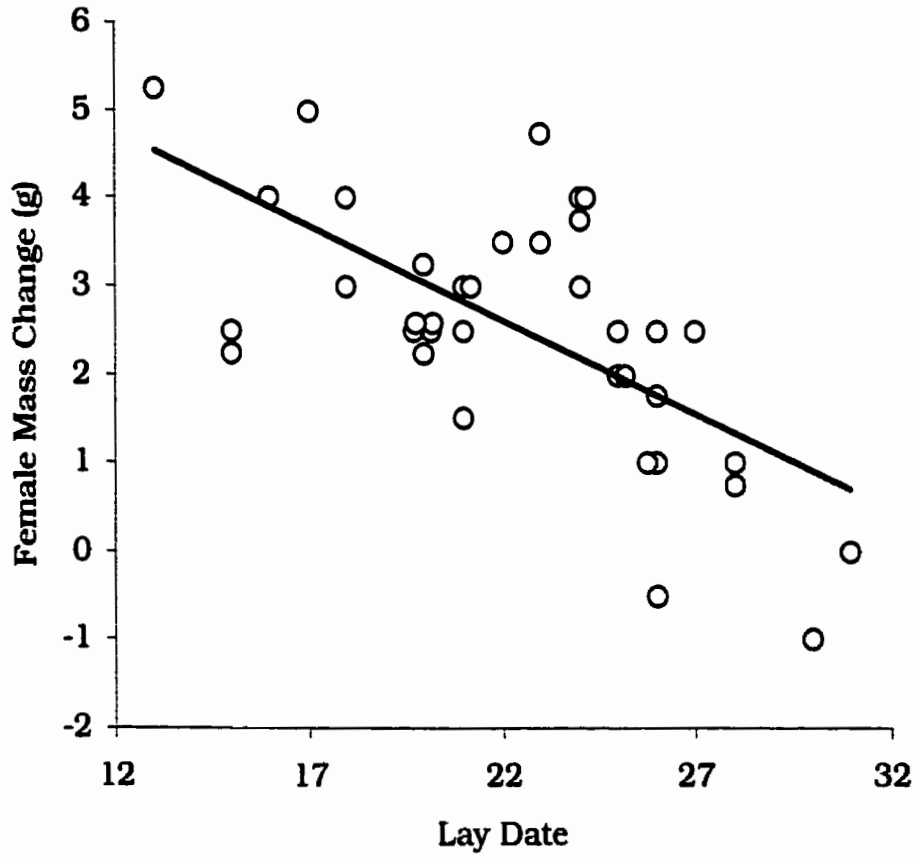


Figure 3.2: Female incubation mass (solid dots) declines significantly with lay date ($p < 0.0001$, $F = 21.46$, $R^2 = 0.333$, $n = 45$) but provisioning mass (open dots) does not decline significantly with hatch date ($p = 0.196$, $F = 1.73$, $R^2 = 0.045$, $n = 39$).

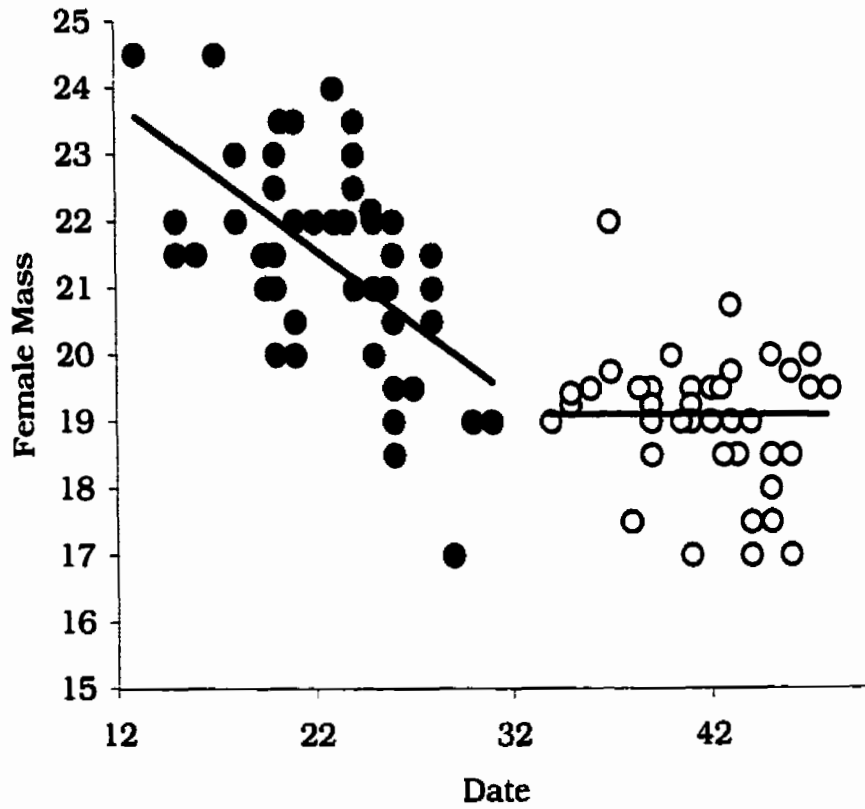
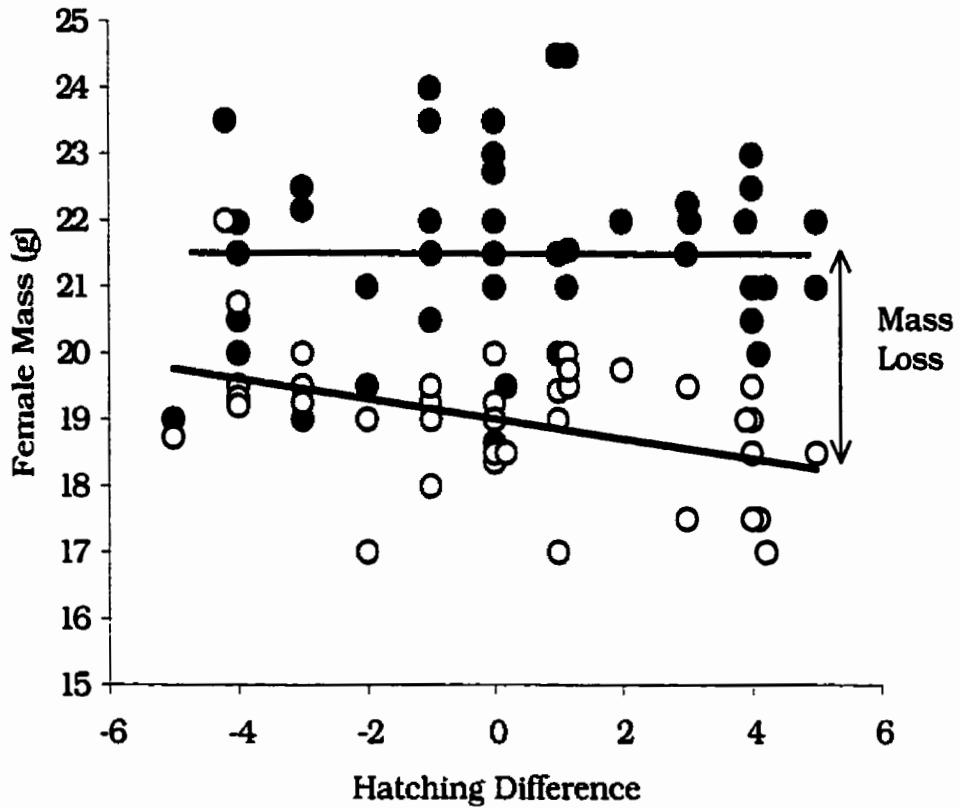


Figure 3.3: Female mass during provisioning (open dots) is negatively correlated with hatching difference ($p=0.004$, $F=9.21$, $r=0.204$, $n=38$) but incubation mass (solid dots) is not ($p=0.286$, $F=1.17$, $r=0.027$, $n=43$).



Discussion

Tarsus length

The significant correlation between nestling and actual mother's tarsus length is evidence of heritable variation in nestling characteristics. This finding is consistent with the results of a study by Wiggins (1989) on this same population of Tree Swallows. Wiggins (1989) found heritability in tarsus length ($h^2=0.50$) and no obvious genetic influence on body mass. The heritability estimate calculated in this thesis was 0.56, only slightly higher than that presented in Wiggins (1989). The discrepancy could be due to the fact that Wiggins (1989) calculated h^2 using correlations between offspring and the average tarsus length of both parents. Due to the reportedly high level of extra-pair paternity in this species, heritability estimates relying on paternal trait values could be underestimates. Nevertheless, heritability of body size is at least 50% in this population.

In contrast, I was not able to assess evidence for heritability of body mass, the performance measure evaluated in this thesis. Other studies of heritability of avian body size tend to find that structural size is highly heritable whereas growth and body mass tend to be more plastic (Merilä 1996, Smith and Wettermark 1995). In the absence of a

link between heritability of body size and nestling performance, there is no way to determine the existence of this effect.

Egg size

I found a positive correlation between egg mass and nestling mass early in the nestling period. However, this effect was not detected in any nestling characteristic by the time nestlings were 15 days old. Egg mass appears to be a maternal effect that translates to heavier nestlings early in the nestling period. Egg size and quality is one of the most commonly investigated maternal effects (Bernardo 1996b, Williams 1994). A number of studies have demonstrated a transitory effect of egg size on nestling size (e.g. Amundsen *et al.* 1996, Meathrel *et al.* 1993, Reid and Boersma 1990) although few have demonstrated whether there are long term fitness advantages to emerging from a large egg (but see Blomquist *et al.* 1997, Hipfner and Gaston 1999). Typically larger eggs produce larger nestlings at hatching, but rarely impact subsequent growth rates (Amundsen *et al.* 1996, Nisbet *et al.* 1998). Therefore, correlations between egg size and nestling mass at day 4 observed in this study likely reflect a residual effect of egg size on nestling size at hatching and may provide an initial but transitory advantage to nestlings. Based on the lack of an effect of egg size beyond day 4 in this population, and evidence from the literature suggesting a lack of maternal effects via egg size in

birds, it seems unlikely that maternal effects can be biasing the interpretation of my hatch-date manipulation experiment.

Though egg size seems unlikely to contribute strongly to nestling performance in birds, it is possible that there are other maternal effects acting via the egg. Reid and Boersma (1990) suggest that the benefits from emerging from a large egg are due to maternal effects via egg composition rather than fitness advantages of emerging from a large egg. A possible mechanism is the passive transfer of antibodies to nestlings via the egg. It is well established that antibodies can be transferred from female chickens to their embryos (Burley and Vadehra 1989), a process called passive immune transfer. If early females have enhanced immune function, they may provide their nestlings with increased protection against parasites and disease. Bishop (1998) demonstrated a seasonal decline in thymus and bursal mass in nestling Tree Swallows, both of which are immunologically active tissues. There is also evidence of seasonal declines in cell-mediated immunity in nestling Tree Swallows (Birmingham unpubl. data). Few studies have as yet looked for evidence of seasonal patterns of immune function in birds, but it is possible that there is a link between immune function and nestling performance. A recent study (Saino *et al.* 1997) demonstrated reduced growth and compromised immune function in enlarged Barn Swallow broods. Enhanced immune function in nestlings could have been transferred via

elements in the egg. I suggest that if passive immune transfer enhances immune responses in nestlings, and this corresponds to increased performance, this would bias towards support for the Date hypothesis in hatch-date manipulation experiments. To date, almost nothing is known about the role of passive immune transfer and nestling immune function in the seasonal decline of nestling performance and is a promising avenue for future research.

Evidence of bias via genetic or maternal effects in the interpretation of the hatch-date manipulation experiment presented in Chapter 2 is not strong. Although there could be unmeasured aspects of both, such as heritability of body mass or passive immune transfer, that may be complicating this interpretation, there is no direct evidence that this is the case. In addition, the only way heritability or maternal effects could cause the observed support for the Date hypothesis early in the season and the Parent Quality hypothesis late, is if the strength of those effects differs at different points in the season. There is no evidence of this in my data and therefore, I conclude that the influence of genetic and maternal effects did not complicate the interpretation of my hatch-date manipulation experiment.

Unintentional impacts of the experiment

Based on data presented in Chapter 2 (Figure 2.4), I concluded that advancing lay date resulted in reduced mass loss. If mass loss in foster mothers influenced nestling performance, then this could cause deviations of the observed performance from that predicted for hatch-date manipulations. There was no detectable effect of female mass loss on nestling mass at day 4, day 15, or nestling tarsus length at day 15. Therefore, it is impossible to know whether mass loss had any impact on the results of the hatch-date manipulation experiment. In addition, without knowing why females lose mass at all, it is not possible to predict what impact experimental adjustments of mass loss should have on nestling performance.

Mass loss between incubation and chick rearing is a common phenomenon in birds. The two main hypotheses to explain mass loss are the reproductive expenditure hypothesis and the flight adaptation hypothesis. The reproductive expenditure hypothesis suggests that mass loss reflects a loss of energetic reserves, as fuel is used up in incubation and provisioning. The flight adaptation hypothesis views mass loss as a strategic adjustment for flight energetics. Flight can be energetically expensive (Drent and Daan 1980, Freed 1981), particularly in aerial insectivores, such as Tree Swallows, who rely heavily on rapid flight and fine scale maneuverability while foraging. Small variations in

wingloading can lead to large provisioning consequences. Unfortunately, in the absence of any link between mass loss and nestling performance, as observed in Blue Tits (Gebhardt-Henrich *et al.* 1998), it is not possible to distinguish which of these hypotheses explains mass loss in Tree Swallows.

Female mass loss declined over the season in 1999. This seasonal decline in mass loss is due to later females having lower incubation masses, as opposed to them retaining higher provisioning masses, as occurred for females that were experimentally advanced in 1999. I suggest that this retention of higher provisioning masses reflected an energetic savings in advanced females due to reduced costs of incubation. Since, by definition, nestlings of advanced females hatched earliest in the season, the observed support for the date hypothesis early in the year could be due to the fact that there were proportionally more advanced females early in the year. These advanced females saved more energy during incubation that could be used during chick rearing. Recent research has experimentally demonstrated that females that expend more energy during incubation produce nestlings with poorer performance than those whose mothers paid lower incubation costs (Reid *et al.* 2000). Unfortunately, I was not able to demonstrate a direct link between female mass loss and nestling performance in this study, so the

role of female mass loss in determining nestling performance remains open to speculation.

Summary

There appears to be evidence of heritability in tarsus length and maternal effects via egg size in this population of Tree Swallows, which would cause a bias towards support for the Date hypothesis. These effects do not appear to influence my performance measure and are probably not responsible for the different hypotheses explaining the pattern of reproductive performance early vs. late in the season. Female mass loss may reflect reproductive expenditure which is the best explanation for why I found support for the Date hypothesis early in the season. However, I was not able to find any link between mass loss and reproductive performance, therefore, the role of mass loss remains ambiguous. The fact that mass loss was clearly impacted by the experiment does underscore the need to assess the impact of hatch-date manipulations on parent quality. Since I did not measure other aspects of parental quality, I can not conclude that unintentional alterations to parent quality did not bias this experiment towards supporting the Date hypothesis early in the season.

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Chapter 4

A literature review of hatch date manipulation experiments

A number of previous studies have manipulated hatch date, either by clutch switching, induced relaying or clutch replacements. Mostly these studies look at seabirds, or a select few passerines. So far, these studies have not found a unifying mechanism to explain the seasonal decline in reproductive performance of temperate breeding birds. The goal of this chapter is to outline why a single mechanism has not emerged from these studies, and suggest how the causes of seasonal declines in reproductive success might better be investigated.

Integrating what is currently known about the causes of seasonal declines in reproductive performance requires a complete overview of the experimental studies that have addressed this question. Table 4.1 is a summary of studies that have experimentally manipulated hatch date, the method used, the trait of interest and the hypothesis supported. Much of this has been summarised previously by Nilsson (1999), but, the summary given here is more complete, and attempts to integrate the results of all of the hatch-date manipulation experiments done to date. Table 4.1 shows that there is support for the Date and Parent Quality hypotheses both within and among species.

Table 4.1: Summary of hatch date manipulation experiments. Numbers refer to individual studies, letters to multiple entries for a single study in the table.

#	Species	Method	Trait	Reference
Parent Quality				
1	Cassin's Auklet	R	Growth	Morbey & Ydenberg 2000
2	Thick-Billed Murre	D	Hatching Success	De Forest and Gaston 1996
3	Thick-Billed Murre	D	Renesting Hatching Success	Hipfner <i>et al.</i> 1999
4	Thick-Billed Murre	D	Growth	Hipfner 1997
5	Herring Gull	E	Fledging Success	Brouwer <i>et al.</i> 1995
6	European Kestrel	E	Fledging Success	Aparicio 1998
7a	European Coot	E	Juvenile Survival	Brinkhof 1995
Date				
8	Common Murre	D	Growth	Hedgren and Linnman 1979
9	Chinstrap penguin	E	Growth	Moreno <i>et al.</i> 1997
10	Snow Goose	E	Growth	Lepage <i>et al.</i> 1999
11	Osprey	D	Fledging Success	Steeger and Ydenberg 1993
12	Blue Tit	D	Growth Fledging Success	Sanz 1999
13	Blue Tit	E	Juvenile Survival	Norris 1993
14	Great Tit	D	Recruitment Rate	Verboven and Visser 1998
15a	Great Tit	D	Recruitment Rate Relaying Rate	Verhulst <i>et al.</i> 1995
16	Pied Flycatcher	D	Growth Fledging Success	Suikamäki 1998
Both				
7b	European Coot	E	Growth Fledging Success	Brinkhof 1995
17	Great Tit	D	Clutch Size Fledging Success Growth	Verhulst and Tinbergen 1991
15b	Great Tit	D	Clutch Size	Verhulst <i>et al.</i> 1995
18	Collared Flycatcher	R	Fledging Success	Wiggins <i>et al.</i> 1994
19	Tree Swallow	E	Nestling Mass	This study
Synchronous breeding only				
20	Common Murre	D	Fledging Success	Hatchwell 1991
21	Herring Gull	D	Hatching Success	Parsons 1975

R = temporary clutch replacement

D = delay via clutch removal

E = clutch exchange

A number of factors might influence the interpretation of hatch date manipulation experiments, including the life history of the species studied, the trait studied, inter or intra-annual variability in climate or food abundance, and unanticipated effects of the manipulation on parent quality. I will discuss these in relation to the results of previous hatch-date manipulation experiments, including the one described in Chapters 2 and 3.

Life History

Aspects of a species life history that could provide insight into the roles of date and parent quality in driving seasonal declines in reproductive performance include parental investment per offspring, the importance of synchronous breeding and territoriality of newly independent offspring.

Per offspring investment

Avian species vary greatly in the amount of energy they invest in each offspring. A group with high per offspring investment are the *Alcidae*, a family of seabirds that are generally long-lived, do not breed every year and rear only one offspring which they provision for a variable amount of time. The most extreme example of low per offspring investment are brood parasites, such as the Brown-Headed Cowbird

(*Molothrus ater*), which do not rear their own offspring at all. In contrast, passerines, such as the Collared Flycatcher, are examples of short-lived birds with low per offspring investment. They generally lay multiple eggs and reproduce every year. Parent quality may be very important in high-investment species. In birds with low per offspring investment, a reduction in parent quality may affect only a portion of that season's offspring, and any effects of parent quality on nestling performance may be difficult to detect. Of the hatch-date manipulation experiments listed in Table 4.1, the highest per offspring investment are found in the alcids (Cassin's Auklet, Common Murre and Thick-billed Murre) and those with the lowest are among the passerines (Blue Tit, Great Tit, Pied Flycatcher, Collared Flycatcher and Tree Swallow). The only alcid study (of 6) that did not support the Parent Quality hypothesis exclusively is one of the Common Murre (Hedgren & Linnman 1979). I will discuss the significance of this later. No study of a passerine (of 8) supported the Parent Quality hypothesis exclusively. These results suggest that the amount of per offspring investment in the species studied affects the likelihood of a hatch-date manipulation experiment finding evidence for the Parent Quality hypothesis.

Unfortunately, the studies done to date are taxa-biased. All of the species with high investment are alcids. Most of the passerine studies were done on two genera (flycatchers and tits) in Europe. Future

research should focus on diversifying the range of species studied. Also, the amount of per offspring investment has not been quantified, and my assessment of investment must be verified. I would suggest a comprehensive meta-analysis in which per offspring investment is quantified by incorporating clutch size, cost of egg production and amount of parental care. These results will then need to be mapped on to a phylogenetic tree.

Synchronous breeding

A number of bird species are highly synchronous breeders and studies of such species are likely to find support for the Date hypothesis if any shift from the peak breeding time results in a reduction in performance. Two-hatch date manipulation experiments suggest that synchronization is the only explanation for seasonal variation in reproductive success (Common Murre, Hatchwell 1991, Herring Gull, Parsons 1975). Two further studies support the Date hypothesis and suggest that synchronous breeding is the most likely explanation for the observed pattern of reproductive performance (Common Murre, Hedgren and Linnman 1979; Snow Goose, Lepage *et al.* 1999). Interestingly, the Common Murre was the only alcid species studied in which Parent Quality did not appear to be the exclusive mechanism driving seasonal declines in reproductive performance. The Common Murre is known to

breed at higher densities and more synchronously than any other species of bird (Hatchwell 1991).

Future studies should employ clutch-switching experiments. If performance is causally linked to date, reproductive success of manipulated birds should follow the usual seasonal trend. But, if synchronous breeding is important, performance should be reduced in both advanced and delayed birds. In experiments that only delay hatch date, it is not possible to distinguish these as predictions about the performance of delayed birds are the same under both circumstances.

Territoriality of independent young

In species in which newly-fledged offspring must settle in a territory following nest departure, date might be the most likely explanation for the seasonal decline in nestling performance because the earliest nestlings have the best access to the available territories. As the season progresses, competition increases and performance declines, due both to the consequences of increased fledgling competition and reduced parental investment in later offspring, whose value is lower. This phenomenon is reviewed in Nilsson (1999). Nilsson (1990) found that establishment success of marsh tits was exclusively determined by prior residency. Establishment success on the wintering grounds may influence juvenile survival to the next season (references in Nilson 1999).

Studies looking at juvenile survival or recruitment in the next breeding season in passerines (Norris 1993, Verboven & Visser 1998, Verhulst *et al.* 1995) support the Date hypothesis. The importance of post-fledging competition in determining seasonal declines in reproductive success is mostly unknown and should be considered in future hatch-date manipulation experiments.

Trait studied

That all studies of passerines looking at juvenile survival or recruitment support the Date hypothesis illustrates the possible importance of the trait studied in interpreting hatch-date manipulation experiments. Traits such as juvenile survival or recruitment are large scale measures of the success of offspring over an entire season. Other variables such as growth, mass, hatching success and fledging success are smaller scale traits that interact to determine the probability of juvenile survival or recruitment. It is possible that parent quality is important at a smaller scale within the nestling period while large scale measures are predominantly driven by date. In fact, in Table 4.1, only one study that looked at a large scale reproductive parameter (juvenile survival, Brinkhof 1995) finds support for Parent Quality or even for both hypotheses. There is no theory available to describe which traits should

be most heavily impacted by parent quality and this is something that should be developed in the future.

Variability in climate or food abundance

There is no doubt that climate and food abundance influence reproductive success. Many food supplementation experiments induce earlier breeding (Högstedt 1981, Arcese & Smith 1988), and a number of studies demonstrate impacts of temperature, rainfall or food abundance on reproductive parameters in birds (Bryant 1975, Erikstad & Andersen 1983, McCarty & Winkler 1999, Murphy 1987). Although it is still not clear that systematic declines in these parameters are responsible for seasonal declines in reproductive performance in birds, variation in them both within and between years could complicate the interpretation of hatch-date manipulation experiments. There are examples in the literature that suggest variation in food abundance could result in different results of hatch date manipulation experiments in the same species. Verhulst & Tinbergen (1991) found support for the date hypothesis in one forest (Forest W) and parent quality in the other (Forest O). Food abundance is higher in Forest O. In situations where there are extremes in temperature and food abundance, those effects may mask the role of parent quality in determining nestling success.

Unanticipated impacts of the experiment on parent quality

Almost all timing experiments assume implicitly that the effects of the hatch-date manipulations on parent quality are minimal, without testing whether this is the case. If manipulations do alter parent quality, these experiments would be biased towards supporting the Date hypothesis, because parents that are delayed have reduced parent quality due to the costs of relaying their clutch or incubating for a longer period. Parent quality of advanced birds might be enhanced due to a reduced cost of a shorter incubation period. If parent quality is altered by timing manipulations, performance will approximate the natural seasonal trend, even when date itself has no influence on performance. My study found that advanced females lost less mass than control or delayed females, which may have contributed to the improved performance of advanced females. Sanz (1999) documented a reduced female body mass in an experiment which induced relaying.

Recent research (Reid *et al.* 2000) has demonstrated that reduced costs of incubation result in improved nestling performance. It is critical that we determine the impacts of the costs of incubation and relaying on subsequent reproductive stages. If impacts of timing manipulations on parent quality are ubiquitous and additional costs early in the nestling period do impact later reproductive stages, then future hatch-date

manipulation experiments may be inappropriate as it would be impossible to interpret them.

Conclusions

The Date and Parent Quality hypotheses yield distinct predictions regarding the outcome of hatch date manipulation experiments. Initial investigations into the mechanisms driving seasonal declines in reproductive performance must have expected a dominant mechanism to emerge from these experiments. Most of these experiments were published over the last 10 years and in that time, an answer still has not emerged. This is likely because there are a number of things that complicate the interpretation of these experiments including life history of the species studied, the trait studied, variability of climate and food abundance both within and between seasons, and more seriously, unanticipated impacts of the manipulation on parent quality. Future research must consider each of these in future studies to most accurately interpret results. Most importantly, we must assess the impact of manipulations on parent quality to assess whether we can ever expect to determine the mechanism driving seasonal declines in avian reproductive performance using timing manipulations.

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General Conclusions

I investigated the roles of date and parent quality in determining reproductive performance in Tree Swallows. I measured performance as nestling mass just prior to nest departure. Parents with a higher capacity or willingness to provision offspring produce higher quality nestlings, and also breed earlier in the season. In order to distinguish between the effects of date and parent quality on nestling mass. I used a clutch switching experiment to manipulate hatch date, producing broods with both advanced and delayed timing. Results of the hatch-date manipulation experiment demonstrate that during the second half of the season, parent quality caused the observed seasonal decline in nestling mass. Early in the season, however, date *per se* was the force driving the seasonal decline in nestling mass.

Hatch-date manipulation experiments are more likely to support the Date than the Parent Quality hypothesis due to biases that mask parent quality effects. Heritability or maternal effects are aspects of parent quality that, when transferred to nestlings, will result in resemblances between nestlings and their actual parents, as predicted by the Date hypothesis. The a priori predictions of hatch-date manipulation experiments are only relevant when the impacts of parent quality on nestling performance occur after hatching. Though there are genetic and

maternal effects transferred to nestlings in the population of Tree Swallows studied in this thesis, they do not appear to impact nestling performance. Unless there were genetic or maternal effects that were not measured in this study that translated into nestling performance, these did not bias my experiment towards supporting the Date hypothesis early in the season.

The hatch-date manipulation experiment presented in this thesis did unintentionally alter female mass loss. This violates the main assumption of these experiments. Unfortunately, it was not possible to determine exactly how female mass loss is connected to female quality, if at all, and there was no evidence that the amount of mass lost impacted nestling performance in any way. Nevertheless, future research must consider any impacts of hatch-date manipulations on parent quality. It is not appropriate to assume that these experiments do not alter parent quality without carefully assessing whether this is the case.

Past attempts at determining the mechanism driving seasonal declines in reproductive performance have produced varying results. There is no clear mechanism emerging from hatch-date manipulation experiments done to date. The role of date vs. parent quality in determining reproductive performance in birds may depend on a variety of characteristics of each system, including the life history of the species studied, inter and intra-annual variation in climate or food abundance,

the scale of the particular trait studied, and any unintentional impacts of the experiment.