EFFECTS OF SHORT-TERM CHANGES IN ENVIRONMENTAL CONDITIONS ON THE FORAGING ECOLOGY AND REPRODUCTIVE SUCCESS OF TREE SWALLOWS, TACHYCINETA BICOLOR

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by John Paul McCarty August 1995 EFFECTS OF SHORT-TERM CHANGES IN ENVIRONMENTAL
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SUCCESS OF TREE SWALLOWS, TACHYCINETA BICOLOR

John Paul McCarty, Ph.D. Cornell University, 1995

Aerial insectivores are known to be highly sensitive to periods of inclement weather during the breeding season. This thesis examines the role environmental variability plays in the foraging and reproductive ecology of an aerial insectivore, the tree swallow *Tachycineta bicolor*, breeding at two sites near Ithaca, New York, USA. Environmental conditions were found to be highly variable on a short temporal scale. The effects of this short-term environmental variability on several aspects of tree swallow biology were documented, and the components of the environment with the greatest influence were identified. Finally, possible adaptations to environmental variability found in tree swallows and other aerial insectivores were investigated.

Tree swallows feeding nestlings foraged in close proximity to the nest and fed exclusively on insects. Adults were highly selective, choosing larger insects over smaller, but diets were diverse. The degree of selectivity was surprisingly constant both among individuals and across a wide range of environmental conditions. Foraging behaviors did differ between two sites studied, and these differences were associated with differences in both nestling growth rates and parental defense behavior.

Several aspects of nestling growth and development were measured, including increase in mass and growth of organs, muscles, feathers, and bones. The changes in metabolic rate and the energetics of thermoregulation associated with growth and development were also measured. Higher growth rates were found to be associated with increased post-fledging survival, and even relatively short-term reductions in growth were found to have significant long-term effects.

Environmental conditions were shown to influence growth rate, with ambient temperature being especially important for the growth of very young nestlings and ambient temperature and food supply being important for older nestlings. Periods of adverse environmental conditions resulted in interrupted growth and nestling mortality. Experimental manipulations showed that the loss of mass during periods of starvation was slower when nestlings' body temperatures fell to near ambient. Measurements in the field showed that wild nestlings do have low body temperatures during periods of inclement weather. The possible adaptive value of flexible body temperatures in nestling tree swallows was also investigated. These results indicate that flexible body temperatures and growth rates may prolong the survival of nestling tree swallows exposed to unavoidable periods of adverse environmental conditions.

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CHAPTER ONE: Introduction

This thesis details studies of the ecology of the tree swallow (*Tachycineta bicolor*) conducted while I was a graduate student in the Section of Ecology and Systematics at Cornell University. Although the range of topics covered in the following chapters is broad, the common theme running through this work is an examination of the role of fluctuations in environmental conditions in the ecology of tree swallows. In this introductory chapter, I will provide a brief overview of the natural history of the tree swallow and describe the role of environmental variability in shaping its ecology.

Tree swallows belong to the family Hirundinidae (the swallows and martins) in the order Passeriformes. The genus *Tachycineta* consists of 8 - 9 new world swallows, most closely allied with the either the bank swallows (*Riparia* spp.), or the new world martins (i.e. *Stelgidopteryx*, *Progne*, *Notiochelidon*; Turner and Rose 1989, Winkler and Sheldon 1993, Sheldon and Winkler 1993). The tree swallow is one of the most abundant swallows throughout its range in North America, and can be found breeding from the western edge of Alaska to eastern Newfoundland, as far north as the tree line. Tree swallows breed across much of the continental United States, except for the southeastern states and the tree-less Great Plains and deserts of the west. In winter, they migrate to the gulf coast of the United States, Mexico, Central America, and the Caribbean (Robertson et al. 1992).

Like all swallows, tree swallows are primarily aerial insectivores, taking insects on the wing during fairly continuous foraging flights. Although

plant material has been reported in the diets of many swallows, the tree swallow is the only species known to be able to subsist for long periods of time on non-insect food, especially the berries of bay-berry (*Myrica* spp.; Beal 1918, Hausman 1927, Bent 1942, Chapman 1955, Place and Stiles 1992). Diet and foraging behavior of this species are addressed in detail in Chapters Two and Three.

Tree swallows are obligate cavity nesters, relying on cavities excavated by other species. Tree swallows prefer to nest in open areas, especially near water. Nest sites near other breeding tree swallows seem to be preferred over solitary nest sites and pairs breeding in loose colonies are more successful than are solitary birds (Sheppard 1977). Currently, natural nest sites occur in cavities in trees adjacent to open bodies of water, and in trees flooded by beaver (*Castor canadensis*). These sites were undoubtedly very important prior to the clearing and settlement of North America by European settlers. Recently, tree swallows have adopted nest-boxes as a preferred nest site (Robertson and Rendell 1990). Cavities are believed to be a limiting resource for secondary hole-nesting birds (von Haartman 1957), including tree swallows (Holroyd 1975, but see Rendell and Robertson 1989), and competition for cavities undoubtedly influences many aspects of the tree swallow's biology.

Tree swallows are the first swallow to arrive in the north each spring and the first to begin breeding (Bent 1942, Sheppard 1977). As a consequence, tree swallows arrive well before the weather is favorable enough to ensure a constant food supply. In central New York, tree swallows typically arrive in the last week in March and must endure several weeks of cold, wet weather, and even occasional snow storms

(McCarty personal observation). Although the tree swallow's ability to forage on bay-berries (Hausman 1927, Bent 1942, Chapman 1955) and to exploit local concentrations of insects (Bent 1942, Dence 1946, Erskine 1984, Cohen and Dymerski 1986, Hobson and Sealy 1987, McCarty MS) undoubtedly increases its ability to withstand these periods, weather related adult mortality is widespread during the pre-breeding period (Dence 1946, Lombardo 1986, Weatherhead et al. 1985, Littrell 1992, McCarty personal observation).

Males tend to return to the breeding ground earliest and defend a nest-site to which they attempt to attract a female (Robertson et al. 1992). Both male and female aggressively defend the area around the nest-site from conspecifics and hetero-specific competitors (Robertson and Gibbs 1982, Lombardo 1987, Robertson et al. 1986, Rendell and Robertson 1991, McCarty personal observation). Pairs defend an area of 10 - 20 m in radius; this area may include more than one nest cavity (Robertson and Gibbs 1982). Nest construction lasts for several weeks in late April and early May at my Ithaca study site. The nest consists of a substantial cup of dry grass, lined with feathers. The number of feathers lining the nest is known to influence reproductive success, possibly by increasing the insulation value of the nest (Winkler 1993).

Egg laying occurs as early as 1 May, and continues until late May. One egg is layed per day until the clutch is completed. Most clutches consist of five or six eggs, with a range of from two to seven. Butler (1988) reported an overall mean clutch size of 5.6 eggs for 13 populations. Clutch sizes of first year females are usually smaller than those of older females (De Steven 1978, Stutchbury and Robertson 1988), and reproductive success is

higher for older females (Sheppard 1977). Incubation usually begins with the penultimate egg, and both laying and incubation may be interrupted by prolonged periods of inclement weather (McCarty personal observation). Females alone incubate during the 14 - 15 day incubation period. Only one brood is raised per year, but most females will re-nest if all or most of the eggs are destroyed (Winkler 1991).

Young generally hatch within a 24 hour period, and are naked, blind, and helpless. Feeding begins soon after hatching, but young are born with yolk reserves that are visible through the skin for about the first three days post-hatching. Only the female broods the nestlings, but both parents share in the feeding of the young (Leffelaar and Robertson 1986, Quinney 1986, Williams 1988, Lombardo 1991, Dunn and Robertson 1992). Extra-pair copulations and fertilizations are frequent (Morrill and Robertson 1990, Lifjeld et al. 1993), but males do not appear to reduce their level of parental care with decreased certainty of paternity (Whittingham et al. 1993). Relative to other non-aerial insectivores, tree swallows expend a large amount of energy in gathering food for their nestlings (Williams 1988), but results of brood manipulation experiments suggest that this effort does not result in dramatically decreased parental survival or subsequent reproduction (Wheelwright et al 1991).

Parents respond to perceived threats to the nestlings by diving at the potential predator and giving alarm calls (Winkler 1992). Both sexes defend the nest against predators, and males tend to defend more aggressively (Winkler 1992). Fledging occurs after approximately 21 days. A fledgling's first flight usually carries it out of sight of the nest, to which most young never return. Parents sometimes continue to provide some

food to the young for at least several days after fledging (D. W. Winkler personal communication).

Reproductive success of tree swallows is strongly influenced by environmental conditions (Quinney et al. 1986, Hussell and Quinney 1987, Dunn and Hannon 1991). Anthropogenic sources of environmental variation are also known to adversely affect reproduction in tree swallows. For example, tree swallows breeding near acidified wetlands have lower reproductive success, possibly due to increased uptake of heavy metals (Blancher and McNicol 1988, St. Louis and Barlow 1993, St. Louis et al. 1993), changes in prey abundance (St. Louis et al. 1990), or difficulty in meeting nestling calcium budgets (Blancher and McNicol 1991, St. Louis and Breebaart 1991). Moderate to high concentrations of several environmental contaminants have been detected in nestling tree swallows (Deweese et al. 1986, Ankley et al. 1993, Bishop et al. 1995), and are associated with reduced reproductive success in some heavily contaminated areas (McCarty and Secord unpublished data).

The following chapters will examine how natural fluctuations in environmental conditions influence reproductive success in tree swallows breeding near Ithaca, New York. An understanding of how environmental factors determine reproductive success, and ultimately population size, is necessary if we are to understand the ecology of wild populations of birds (Newton 1991). Such an understanding will require the integration of both temporal and spatial variation on a range of scales, and knowledge of how individuals respond to different types of environmental variation. Tree swallows are subject to variation in a

variety of environmental variables, and such variation occurs both predictably, and unpredictably.

In the following chapters, I first describe the foraging ecology of this species (Chapters Two and Three). Since nestling energetics play an important role in determining the effects of the environmental variations, I present a detailed summary of nestling energetics and thermoregulation (Chapter Four). Growth rate is shown to be a good indication of subsequent survival in tree swallows, and Chapter Five documents environmental effects on growth and development. The effects of shortterm changes in growth rate on overall growth in tree swallows are also examined (Chapter Five). Chapter Six explores the importance of fat stores and other aspects of body composition in determining the survival of nestlings during periods of adverse weather. Finally, I examine the relative importance of fluctuations in food supply and ambient temperature on nestling growth rates using path analysis (Chapter Seven), thereby providing both a framework for the evaluation of the relative importance of different means of coping with environmental variation and a powerful means of generating hypotheses and predictions about tree swallow life history.

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CHAPTER TWO: Foraging Ecology of Tree Swallows: Site Use, Diet, and Prey Selection.

"The primary driving force of all animals is the necessity of finding the right kind of food and enough of it. Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food supply."

Charles Elton, 1927

INTRODUCTION

The study of foraging ecology is a central component to the understanding of the ecology and behavior of species (Grinnell 1917, Crook 1964, Huey and Pianka 1981, Shields et al. 1988, Emlen and Wrege 1991), as well as being the basis for studies of community ecology (MacMahon et al. 1981, Koehl 1989, Wiens 1989). Food is thought to be an important limiting factor on populations and distributions of birds (Lack 1954; Martin 1986, 1987; Safina et al. 1988; Monaghan et al. 1989; Rodenhouse and Holmes 1992), and patterns of food resource exploitation have been shown to be important in understanding avian community structure (MacArthur 1958, Lack 1971, Wolf et al. 1976, Feinsinger and Colwell 1978, Grant and Schluter 1984). Variation among individuals in foraging is linked to variation in reproductive success (Pierotti and Annett 1987, Wunderle 1991) and survival (Weathers and Sullivan 1989). Such variation in the components of fitness may be important in explaining the divergence (Smith 1990a, 1990b,1993) and eventual speciation of populations (Lack 1947, Grant 1986, Benkman 1993).

In this chapter I describe the foraging ecology and diet of the tree swallow (*Tachycineta bicolor*). Tree swallows are obligate aerial insectivores and members of a distinct guild which forages on insects in the air column. Hirundines have proven to be valuable subjects for the study of foraging behavior and ecology (Bryant 1973; Bryant and Turner 1982; Turner 1982b; Brown 1986, 1988a, 1988b; Stutchbury 1988; Hebblethwaite and Shields 1990) because their feeding behavior is relatively easy to observe and because their prey resources are relatively easy to identify and sample accurately (Southwood 1978, Cooper and Whitmore 1990).

Foraging theory makes predictions about what kinds of food items an individual should include in its diet and how diet should change with changes in prey availability (Emlen 1966, MacArthur and Pianka 1966, Krebs 1978). I test two specific predictions of these models: that individuals should include only the most profitable items in their diet and that individuals should become more selective as food becomes more abundant. In addition, I examine how selectivity changes with increasing demand from nestlings as they grow and develop, and whether males and females differ in the types or sizes of food they deliver to their nestlings.

Most studies of avian foraging focus on a single site and last fewer than three years. Environmental conditions that influence foraging change over several different temporal and spatial scales, and the effects of most of these changes on conclusions drawn from a single study are unknown. The study described in this chapter attempts to address these potential problems in several ways. Foraging behavior and diet were examined at two different sites and over five seasons. To look for

differences in behavior and diet across a much larger geographic scale I compare the results of the present study to those of previous studies conducted at several locations throughout the species range.

METHODS

General Methods and Study Site

Tree swallows breeding in nest-boxes were studied at two sites near Ithaca, New York (42° 30' N 76° 27' W). These sites are part of the Comell University Experimental Ponds Facility; both consist of large, flat, open, grassy areas with regularly spaced man-made ponds and a large, marshy lake. The sites are surrounded by forest and abandoned farm fields. Nest-boxes are mounted on poles approximately 1.5 m above ground and are equipped with conical metal predator guards. Most boxes are within 2 m of open water and are spaced 20 m apart. Unit One is a 13-ha site with 41, 0.1-ha ponds and a 6-ha lake. There are 105 nest-boxes at this site, used by 55 - 75 pairs of breeding swallows. Unit Two is a 20-ha site with 50 0.1-ha ponds and a 7-ha lake. Starting in 1990, 10 nest boxes were erected at Unit Two, each spaced 40 m apart. In 1991 and 1992 there were 22 boxes available, and 27 boxes were available in 1993. Breeding pairs ranged from 10 in 1990 and 1991 to 23 pairs in 1993.

Insect Sampling

Suction traps are the best available method for minimizing bias in the measurement of the abundance of aerial insects (Johnson 1950, Taylor 1962, Service 1977, Southwood 1978, Muirhead-Thomson 1991). A 12.2 m

Rothamsted Aerial Insect Trap (Macaulay et al. 1988) located at Unit One was used from 1989 - 1993. By sampling at 12 m, the Rothamsted trap avoids most of the effects of local emergence events, giving a good estimate of overall insect density (Taylor and Palmer 1972). The Rothamsted trap design has been used extensively for monitoring of insect pests (Taylor et al. 1981, Woiwood et al. 1984), in studies of insect migration and dynamics (Taylor 1986), and in previous studies of Hirundine ecology (Bryant 1973, Bryant and Turner 1982, Turner 1982). The efficiency of this trap design for studies of tree swallow foraging is discussed in detail in Appendix One.

Daily samples were collected in 70% ethanol between approximately 0630 h and 1730 h during the swallow breeding season (approximately 1 May through 25 July). Insect samples were examined under a dissecting microscope and identified to order, with the exception of Diptera, which were identified to sub-orders Nematocera and Brachycera. Small numbers of spiders (Aranae) were found in both the suction trap and diet samples; these have been included in the subsequent analyses in the Other Taxa category. Large numbers of thrips (Order Thysanoptera) occasionally occur in the suction trap samples, however due to the small size of thrips (usually < 0.5 mm) and the fact that they were never observed in swallow diets, all subsequent analyses exclude thrips. Insects were sorted into size categories of 0-3, 3-5, 5-7, 7-9, 9-11, 11-13, and > 13 mm in length (excluding antennae and ovipositors). Body lengths were converted to mass by sorting fresh insect samples into the categories described above and drying them in an oven to a constant mass (e.g. ± 0.01 mg). Samples were

Table 2.1 Insect masses used in converting insect lengths to mass. Mass is the mean mass of lots of 1-40 insects weighed as a group and divided by the number of individuals in a lot. Standard deviations are given for the mean of lots. Mass in mg, Size = length in mm, n = the number of total individuals in all lots for each category. "Mixed Arthropods" includes the Orders Araneae, Coleoptera, Hymenoptera, Orthoptera, Plecoptera, and Trichoptera.

Taxon	Size	Mass	Stdev	# Lots	<u>n</u>	
Mixed Arthropods	0-3 3-5 5-7 7-9 9-11 11-13	0.494 1.559 3.150 7.925 15.016 33.841	0.217 0.834 1.603 6.477 7.616 4.382	9 11 11 8 3 2	34 51 36 17 7 3	
Hemiptera	0-3 3-5 5-7 7-9	0.434 1.865 3.756 3.290	0.062 1.174 0.538	3 2 4 1	33 21 47 2	
Diptera- Nematocera	0-3 3-5 5-7 7-9 17-21	0.353 0.601 0.652 1.654 12.210	0.052 0.131 0.076 1.458	6 5 7 2 1	90 59 235 5 1	
Diptera- Brachycera	0-3 3-5 5-7 7-9 9-11	0.378 0.929 2.650 4.990 2.985	0.105 0.065 1.162 1.155	8 3 5 3 1	183 46 80 19 2	
Odonata- Anisoptera Zygoptera		37.355 5.668	23.379 3.478	22 116	22 116	

weighed to the nearest 0.01 mg using a Mettler Analytical Balance and these values used to convert the insect length values to dry mass (Table 2.1).

Foraging Site Use

The use of foraging sites by adult tree swallows feeding young was quantified using focal-nest observations in 1990, 1991, and 1992. In 1990 and 1991, the focus of the observations was the use of horizontal space by the swallows. For these observations, each breeding site was divided into several foraging habitats (i.e. over ponds or over fields), and fifteen or thirty minute focal observations were done on breeding pairs. During observations, the observer waited until an adult left the nest and recorded what habitat type(s) the swallow foraged over and the time spent over each type (to the nearest minute). The observer continued to follow the focal bird until it returned to the nest or was lost from sight. If the observer lost sight of the swallow, the time at which it was last seen was recorded along with information on the sex of the forager (if known) and the reason the bird was lost (i.e. it left the Pond Unit or the observer was no longer sure which foraging swallow was the focal bird). In 1992, information about horizontal use of space was recorded, but observations focused on the vertical strata used by the swallows. The air column was divided into three strata (0-2 m, 2-12 m, > 12 m) and observers recorded the use of each stratum to the nearest second, using lap-top computers running an event recorder program. The limits of vertical strata were based on observations in 1990 and 1991 and the availability of good reference objects of known height to aid height measurements in the field. Simultaneous

observations of the same birds by two or three observers confirmed that all observers were able to consistently identify the strata a swallow was using. All pairs in the population were observed for a 30 minute period on either nestling day 3, 9, or 12. As in previous years, an adult was watched as it left the nest and its use of strata recorded until it returned to the nest or was lost from sight. After the focal bird returned or was lost, information on its identity, use of foraging site, and reason for ending the observation (i.e. bird returned or was lost) were recorded. For each nest, the percentage of time spent in each vertical stratum and the percentage of time foraging at the breeding site was calculated.

Diet Sampling

Samples of nestling tree swallow diets were obtained using two methods. Adult tree swallows collect a bolus of insects before returning to feed the young. Each year most adults were captured during the nestling period using nest-traps. When an adult was captured, all insects in its mouth were removed, and the nest was inspected for food items that had been dropped (Quinney and Ankney 1985, Blancher et al. 1987). The sex of the parent was recorded and the samples stored in 70% ethanol.

In 1989 and 1990 diet samples were also obtained using an artificial nestling puppet. For this technique, an observer in a blind placed directly behind a nest operated an artificial nestling puppet and would compete with the live nestlings for the insect boluses brought by the adults. When the adults fed the puppet, it was quickly withdrawn from the nest and the bolus removed. For a more detailed description of this technique, see McCarty and Winkler (1991). All diet samples were sorted using the

method described for the aerial insect samples above. Results of these two sampling methods are compared in Appendix One.

Analysis of Selectivity

The insects chosen by the swallows were compared to the insects available in the air column on the day the sample was obtained. If use differed from availability, selection for or against the resource is said to have occurred (Chesson 1978). Several indices have been proposed to evaluate the use of resources by animals in relation to the resources available (Ivlev 1961; Manly 1974; Chesson 1978, 1983; Johnson 1980; Lechowicz 1982; Alldredge and Ratti 1986, 1992). I use the method presented by Manly et al. (1993) for estimating selectivity ratios when samples of available and used resources are available for different individuals. This index has several advantages over alternative indices; 1) it uses individual samples as the unit of comparison, 2) it is insensitive to the number of categories included, and 3) it produces indices which can be easily interpreted. Selection ratios were calculated for each sample using the equation:

$$\hat{w}_{ij} = \frac{u_{ij}}{\hat{\pi}_{ij} u_{+j}} \tag{2-1}$$

(Manly et al. 1993, eq. 4.42), where the selection ratio, \hat{w}_{ij} for category i is calculated for each sample j; u_{ij} is the number of prey items in category i found in sample j; u_{+j} is the total number of items in sample j, and $\hat{\pi}_{ij}$ is the proportion of the total food items available when sample j was

collected that were in category i. The population selection ratio for category i is then calculated by combining the ratios for each sample using:

$$\hat{w}_{i} = \frac{u_{i+}}{\sum_{j=1}^{n} \hat{\pi}_{ij} u_{+j}}$$
 (2-2)

(Manly et al. 1993, eq. 4.43), where u_{i+} is the total number of items in category i for all n samples. The standard error of \hat{w}_i is calculated according to Manly et al. (1993, eq. 4.14). The null hypothesis that $\hat{w}_i = 1$ was tested by comparing $((1-\hat{w}_i)/\text{se}(\hat{w}_i))$ to the appropriate critical value from the standard normal distribution, using a Bonferroni adjustment for multiple comparisons (Manly et al. 1993).

The standardized selection ratio, B_i , was then calculated from Manly et al. (1993) equation 4.10, with the exception of the B_i values given in Table 2.7. Since the raw data on individual samples from other studies were not available, the comparisons across studies in that table are based on samples pooled within studies (Manly et al. 1993, eq. 4.22).

The selection ratio, \hat{w}_i , can be interpreted as a ratio of use to availability, where $\hat{w}_i = 1$ indicates that no selection is occurring. The standardized selection ratio, B_i , can be interpreted as the expected relative contribution of the food type to the predator's diet if all food types were equally abundant.

RESULTS

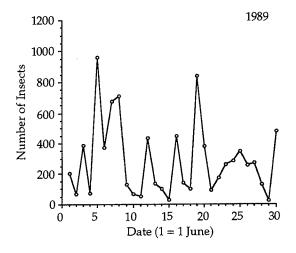
Insect Sampling

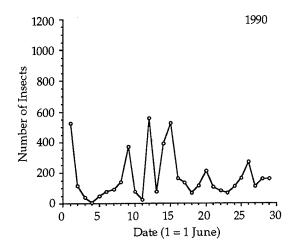
Insect abundance did not change systematically with date during the main nestling-rearing phase in June in any of the five years analyzed (Figure 2.1; least squares regression, p > 0.20 for each year). However, there was a large amount of day-to-day variation in insect abundance, with daily catches differing by as much as two orders of magnitude (Figure 2.1). The insect fauna consists of a large proportion of insects less than 3 mm long (Figure 2.2). Nematoceran Dipterans make up over half of the June samples, with Brachyceran Dipterans and Hemiptera (= Homoptera + Heteroptera) being next in abundance (Figure 2.3). Arthropods from at least eight other orders make up the remaining insect catch (Table 2.2).

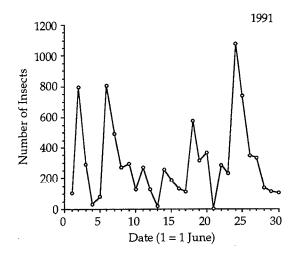
Foraging Site Use

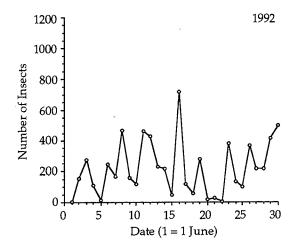
Foraging swallows generally remained near the breeding area, foraging in open areas over fields and ponds. A swallow was considered to be "on site" when it was foraging within the confines of the Ponds Unit (delineated by a 2 m fence) and was "off-site" if it was observed leaving the Ponds Unit. During focal nest observations, tree swallows spent about 12% of the foraging time off site, 40 - 100% of the period within view on site, and the remainder of the period lost from view but with no evidence that they had left the site (Table 2.3). The exception to this was observed in 1990 when swallows at Unit One spent a significant amount of time off site. During this period I observed many swallows foraging over old fields approximately 100 - 300 meters from the breeding area. There are significant differences between the two Ponds Units in the percent of time

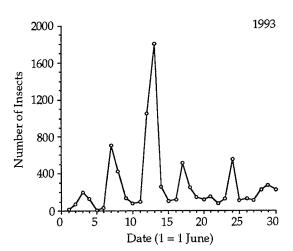
Figure 2.1. Daily insect catch from the 12 m Rothamsted Suction Trap. Each point represents the total number of insects caught during the daylight hours during June. Insect abundance shows no overall increase or decrease with date (linear regression, p > 0.20 in each year). Note different scale for 1993.

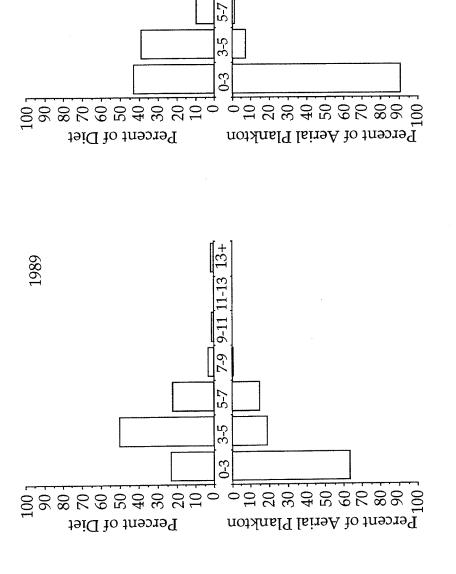








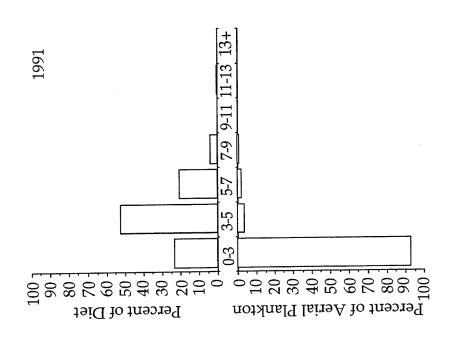


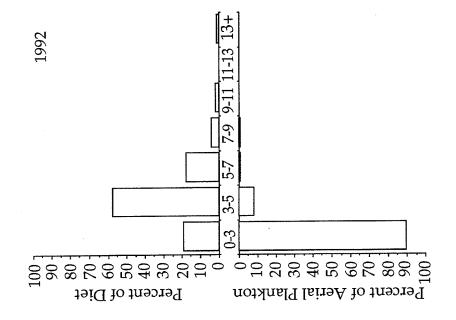


1990

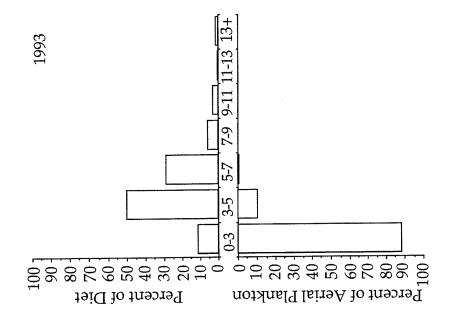
Figure 2.2. Comparison of the distribution of insect sizes found in tree swallow diets to the sizes of insects available in the aerial plankton, for each year. Proportions are based on the number of samples were obtained are included; if more the one diet sample was obtained in a day, the insects in each category for each bolus or suction trap sample. The average of these sample proportions for each year is given. For the aerial insect distributions, only days when diet suction trap data for that day are included more than once.

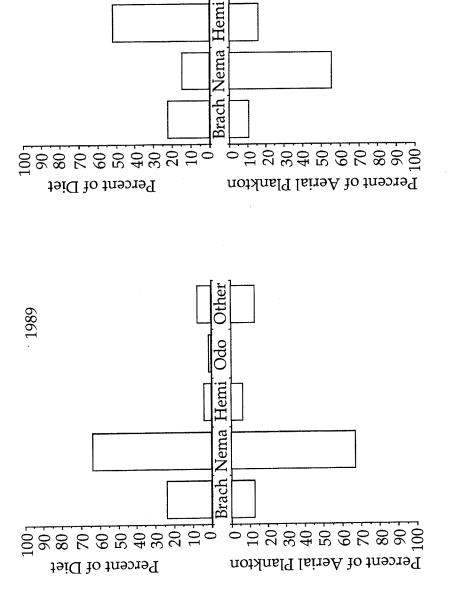




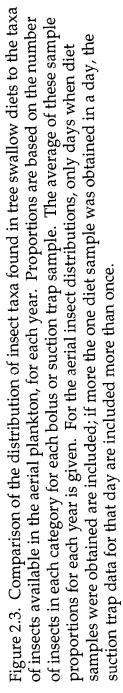




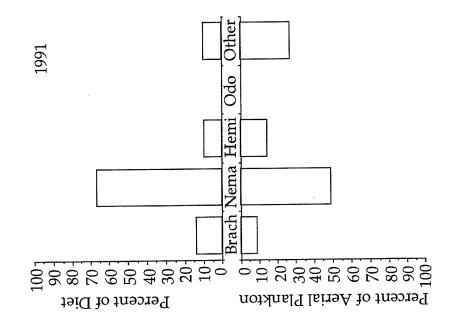


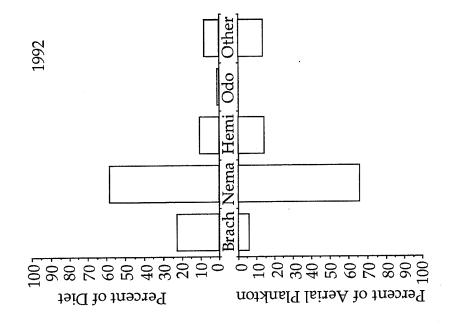


Other











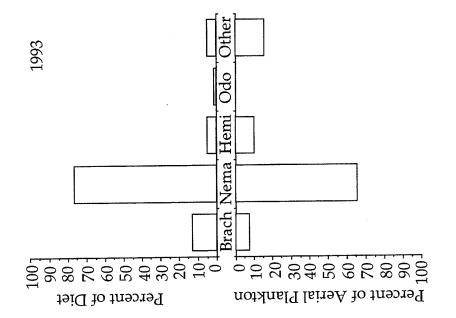


Table 2.2. Invertebrate taxa present in the aerial plankton and taxa in tree swallow diets. Presence of taxa below the level of order indicates that these taxa have been identified as present, but does not mean that no other families in those orders are present.

Class Arachnidae Order Araneae Class Insecta Order Ephemeroptera O. Odonata S. O. Anisoptera F. Libellulidae F. Coenagrionidae O. Plecoptera O. Psocoptera O. Hemiptera S.O. Homoptera F. Cicadellidae F. Corcopidae F. Cicadellidae F. Aphidae S. O. Heteroptera F. Nadidae F. Nadidae F. Nadidae F. Nadidae F. Lygaeidae O. Thysanoptera O. Coleoptera O. Diptera S. O. Nematocera F. Tipulidae F. Chaoboridae F. Chaoboridae F. Chironomidae S. O. Brachycera O. Hymenoptera C. Diptera C. Diptera C. Disptera	<u>Aerial Plankton</u>	Tree Swallow Diet
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Table 2.3. Comparison of the percent of foraging trips remaining within the study area for each breeding site in each year. N is the number of observation periods (each observation period counts as one observation in the ANOVA), and n is the mean number of foraging trips per observation period.

Site	1990	1991	1992	
Unit 1	40.2 ± 8.4	60.3 ± 10.8	78.0 ± 3.5	
N (n)	19 (4.6)	8 (5.1)	70 (4.9)	
Unit 2	97.4 ± 2.6	100.0 ± 0	95.5 ± 2.1	
N (n)	13 (4.5)	8 (5.9)	31 (4.6)	
p- Value	0.001	0.002	0.002	

spent foraging at the breeding colony, with swallows at Unit Two spending significantly more time on site than those at Unit One in all three years (Table 2.3). This result underestimates the differences in foraging site use, since the area defined as on-site was smaller at Unit Two than the at Unit One.

Tree swallows spent the majority of their time foraging between 0 and 12 meters above the ground (Figure 2.4). Swallows spent less than 20% of their time foraging above 12 m, significantly less than the proportion of time spent below 12 m (paired t-test = 9.597, p < 0.001). The proportions of time spent in each stratum did not differ between sites.

Nestling Diet

215 diet samples were obtained between 1989 and 1993. These samples were obtained between 4 June and 17 July, with 86% obtained in June. Comparing the hatch days of the nests from which diet samples were taken to the hatch days of the population as a whole, more samples were obtained from later hatching nests than would be expected (ANOVA F = 29.6, p = 0.001). Samples were taken from nestlings as young as day two and as old as day 16 (mean = day 10). Sampling effort was concentrated, however, in the middle of this range, with 51 % of samples being obtained between days 8 - 12 inclusive, 23 % from nestlings younger than day 8, and 25 % from nestlings older than day 12.

Tree swallow diets consisted of a wide range of insect sizes from at least eleven orders (Table 2.2). Sizes ranged from insects less than 1 mm in length to large Anisopteran Odonates over 30 mm in length. Insects in the 3 - 5 mm class made up the largest proportion of the diet by numbers

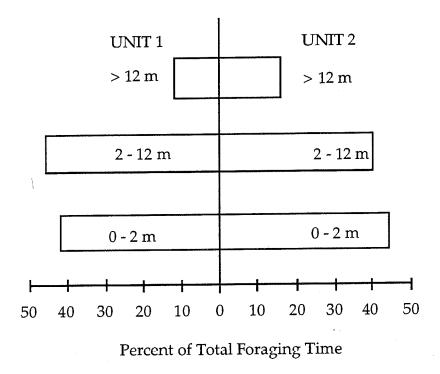


Figure 2.4. Proportion of time spent foraging at different heights by tree swallows feeding nestlings. Based on 72, 30 minute focal nest observations at Unit One and 33 focal nest observations at Unit Two. Differences between Ponds Units are not significant (ANOVA p > 0.20). Proportion of time spent below 2 m and between 2 m and 12 m are not significantly different (paired t-Test, p > 0.79). Amount of time spent foraging above 12 m is significantly less than time spent below 12 m (paired t-Test, p < 0.001).

(Figure 2.2), and on a dry mass basis (Figure 2.5). Diptera were the most frequently eaten taxa, with Hemiptera and Odonata also making up a significant part of the diet (Figure 2.3). None of the other orders accounted for more than 5% of the total diet by number. Diptera were the most important taxon based on dry mass (Figure 2.6), although Hemiptera, Odonata, and Other Taxa are almost equally important.

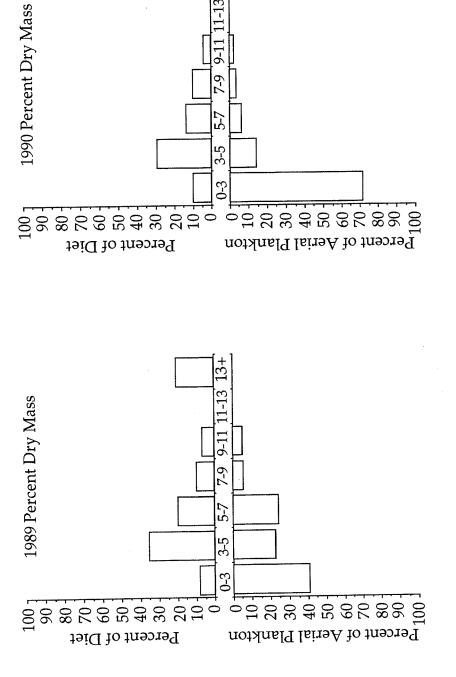
The sex of the adult from which a sample was obtained did not influence the size or taxonomic composition of the sample (Table 2.4).

Selectivity for Size and Taxa

The selection ratios, w_i , indicate that insects in the 0-3 mm size range are selected against (i.e. w_i , < 1) and that larger insects are selected for, with the probability of selection generally increasing with the size of the insect (Table 2.5). Nematocera and Other Taxa are selected against, while there is selection for Odonata and Brachyceran Diptera. Tree swallows also show significant selection for Hemiptera, but the preference is weak with Hemiptera generally being eaten in proportions similar to their availability (Table 2.5).

<u>Changes in Selectivity with Nestling Age, Date of Sample, and Insect Abundance</u>

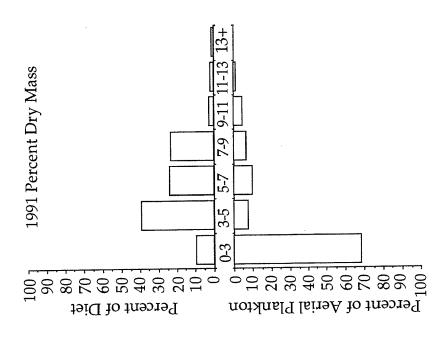
There were few changes in selectivity with age of the nestlings being fed, date, or insect availability (Table 2.6). Only for insects less than 3 mm in length did selectivity change significantly with age. Even though it appears that these small insects were incorporated more in diets of older chicks, the multiple regression explains only a small amount of the

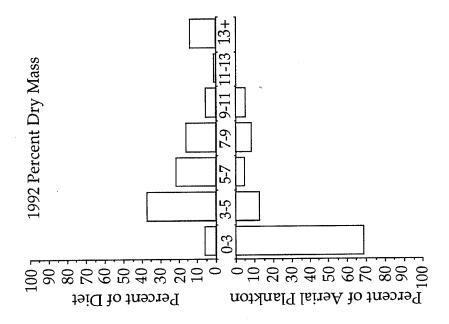


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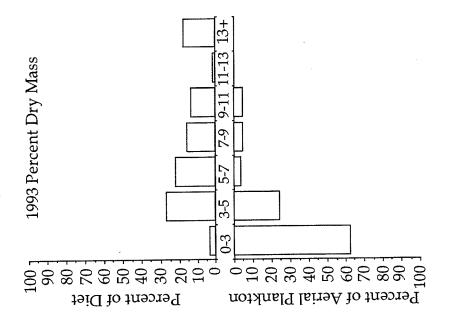
of these sample proportions for each year is given. For the aerial insect distributions, only days contribution to the insects available in the aerial plankton, for each year. Proportions are based when diet samples were obtained are included; if more than one diet sample was obtained in a on the dry mass of insects in each category for each bolus or suction trap sample. The average Figure 2.5. Comparison of contribution of insect size categories to tree swallow diets to day, the suction trap data for that day are included more than once.

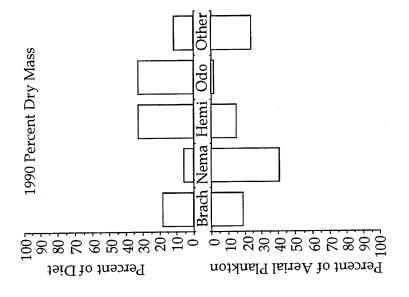












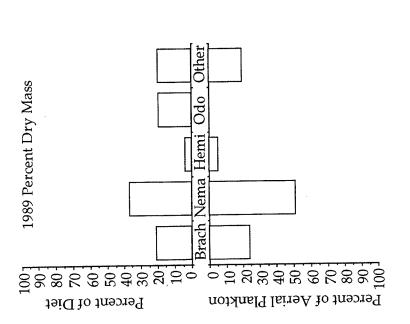
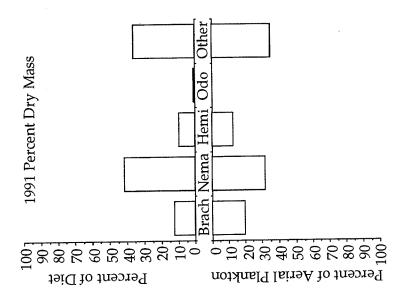
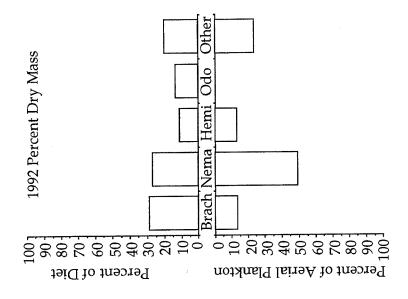


Figure 2.6. Comparison of the contribution of insect taxa to tree swallow diets to contributions sample proportions for each year is given. For the aerial insect distributions, only days when to the insects available in the aerial plankton, for each year. Proportions are based on the dry diet samples were obtained are included; if more the one diet sample was obtained in a day, mass of insects in each category for each bolus or suction trap sample. The average of these the suction trap data for that day are included more than once.

Figure 2.6 (continued)







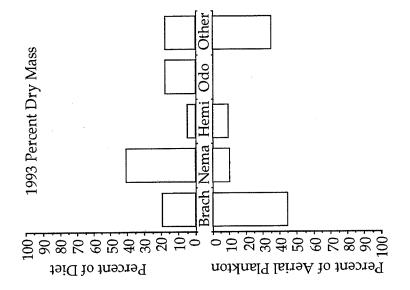


Table 2.4. Comparison between the composition of diet samples obtained from male and female parents. Values given are means of percents \pm 1 SE. n=107 for females and n=91 for males. p - values for student's t-tests. None of the means are significantly different when adjusted for multiple comparisons.

Taxa	Male	Female	p - value
Diptera - Nematocera	27.7 ± 3.8	26.5 ± 3.5	0.819
Diptera - Brachycera	29.8 ± 3.6	31.7 ± 3.4	0.702
Hemiptera	17.5 ± 3.2	17.9 ± 2.9	0.925
Odonata	13.0 ± 3.4	14.2 ± 3.2	0.804
Other Taxa	12.1 ± 2.6	9.8 ± 2.1	0.487
Size (mm)			
0-3	19.0 ± 2.7	18.7 ± 2.4	0.934
3-5	44.3 ± 3.5	34.2 ± 3.0	0.029
5-7	12.5 ± 1.8	17.8 ± 2.5	0.094
7-9	4.7 ± 1.0	6.3 ± 1.6	0.426
9 +	19.5 ± 3.9	23.0 ± 3.7	0.512

Table 2.5. Components used in calculating selectivity for insect taxa and sizes in tree swallow diets. Diet samples from 1989 -1993 pooled, n = 213 samples. $u_i =$ number of items in category i used, $m_i =$ number of items of category i available, $w_i =$ selection ratio, $se(w_i) =$ standard error of w_i , and $B_i =$ selection index standardized to minimum of 0, maximum of 1.0. Selection ratios, w_i , calculated from selection ratios for each sample (for further details see text). * next to w_i indicates a selection ratio significantly different from 1, using Bonferroni adjustment for multiple comparisons (overall $\alpha < 0.05$).

Size	иi	m i	w_i	(se(w _i))	<i>B</i> _{<i>i</i>}
0 - 3	995	56061	0.289*	(0.002)	0.009
3 - 5	1926	7191	6.295*	(0.051)	0.207
5 - 7	704	2540	8.290*	(0.122)	0.272
7 - 9	149	314	6.023*	(0.119)	0.198
9 +	106	183	9.582*	(0.178)	0.314
<u>Taxa</u>					26
Nematocera	2005	39840	0.842*	(0.005)	0.020
Brachycera	780	7410	2.015*	(0.017)	0.048
Hemiptera	728	9158	1.348*	(0.014)	0.032
Odonata	57	19	37.500*	(1.167)	0.887
Other	310	9802	0.552*	(0.006)	0.013

Table 2.6. Change in selectivity, w_i , with age of chicks being fed, date, and total food availability. Diet samples from 1989 -1993 pooled, n= 206 samples. For each category of dependent variable, the overall adjusted multiple \mathbb{R}^2 (and p-value) is given, as well as the standardized partial regression coefficients (and p-values) for age, date, and food availability.

Category	overall <u>R</u> 2	age	date	food available
0 - 3 mm	0.03	0.17	0.02	0.04
	(0.095)	(0.018)	(0.801)	(0.577)
3 - 5	0.05	0.08	-0.04	-0.20
	(0.019)	(0.286)	(0.590)	(0.005)
5 - 7	0.04	-0.14	-0.09	0.08
	(0.112)	(0.105)	(0.273)	(0.324)
7 - 9	0.01	0.04	-0.05	-0.03
	(0.922)	(0.679)	(0.638)	(0.793)
9 +	0.22	-0.01	0.40	2.52
	(<0.001)	(0.956)	(<0.001)	(0.007)
Nematocera	0.05	-0.10	-0.17	0.01
	(0.023)	(0.157)	(0.020)	(0.923)
Brachycera	0.04	-0.14	-0.10	0.02
	(0.047)	(0.051)	(0.147)	(0.763)
Hemiptera	0.06	0.07	0.21	-0.04
	(0.009)	(0.354)	(0.004)	(0.611)
Other	0.01	0.10	0.03	0.02
	(0.497)	(0.185)	(0.667)	(0.743)

variance ($R^2 = 0.03$). Selection for 5-7 mm insects decreases slightly with age, but is not significant (p = 0.105) The selection for both Brachyceran and Nematoceran Diptera shows a negative relationship with age, but again the coefficients are not significant.

Insects in the largest size group showed increasing selectivity with date of the samples (Table 2.6). There were also significant changes in the taxonomic composition of the diets with date, with selectivity for Nematoceran Diptera decreasing over time and selectivity for Hemiptera increasing with date.

Total insect availability had little effect on selectivity (Table 2.6). Selectivity for insects in the 3-5 mm range decreased with increasing overall insect abundance, and selectivity for insects larger than 9 mm increased with increasing insect abundance. Although the multiple regression for the 3-5 mm category explained little of the variance in selectivity (overall $R^2 = 0.05$), the regression for the > 9 mm category did explain a significant portion of the variance in selectivity (overall $R^2 = 0.22$), with a partial regression coefficient for insect availability of 0.25.

DISCUSSION

Although they exhibit diverse foraging strategies during the non-breeding season (McCarty MS, Bent 1942, Chapman 1955, Cohen and Dymerski 1986), during the breeding season tree swallows rely almost entirely on aerial insects captured during prolonged cruising flights.

Analysis of site use indicates tree swallows tend to forage within 100 - 200 m of their nest, at altitudes below 12 m (Table 2.3, Figure 2.4). The breeding

sites in the present study were mosaics of ponds and land, and the swallows moved freely from one habitat to another in the course of a single foraging bout. This pattern of foraging behavior is similar to that reported in studies of tree swallow foraging from other areas (Holroyd 1972, 1983; Quinney and Ankney 1985; St. Louis et al. 1990). This pattern of foraging site use indicates that tree swallows at the sites studied here are foraging in the same habitat where resource availability was measured. Swallows spend most of their time foraging at their breeding site (Table 2.3) and do not spend significant time at extreme altitudes (Figure 2.4). The measure of site use in Table 2.3 is conservative because it includes only the time spent at the breeding site and while in view of the observer; time out of view of the observer has been lumped with time away from the breeding site resulting in an overestimate of the amount of foraging away from the breeding site. Although tree swallows do spend some time foraging away from the breeding site, my observations on site use, combined with the high rates of feeding visits to nestlings, indicate that tree swallows spend most of their foraging time very near the breeding site.

Insects available can also vary on a smaller spatial scale. In the vertical dimension, insect abundances do vary, with abundance decreasing with altitude (Appendix One). However, abundances at different altitudes are highly correlated over time. Differences in insect abundance at different altitudes thus should not influence my conclusions. The proportions of different taxa in the insect community also change with altitude (Appendix One). The effect of these changes on my conclusions are discussed under "insect selectivity" below. Insect distributions may be

patchy on smaller scales in the horizontal dimension as well. The 12 m Rothamsted trap is designed to be tall enough to obtain a homogenized sample that is relatively immune to small-scale patchiness (Taylor and Palmer 1972), and the analyses in Appendix One indicate that the twelve-hour samples used in this study are not unduly influenced by the effects of small-scale patchiness in insect abundance.

Nestling Diet

Nestlings were fed a diverse array of insect taxa and sizes (Table 2.2, Figure 2.2), and parents were highly selective in their choice of insects (Table 2.5). Although this study measured only the diets of nestlings, studies comparing the diets of adult and nestling Hirundinidae have generally found the two to be similar (Stoner 1936; Turner 1982b, 1983; Blancher and McNicol 1991).

Adults captured large numbers of relatively small insects (< 3 mm), especially Nematoceran Diptera. Nematocera make up over half the items brought to the nest in each year (Figure 2.3), but make up considerably less of the biomass delivered (Figure 2.6). The selectivity for insects larger than these small Nematocera (Table 2.5) may suggest that the relative profitability of available insects is correlated with size.

The selectivity measures are based on availability as measured by the 12 m sample. However, the proportions of different insect taxa in the air column changed with altitude, with Hemiptera becoming more abundant with altitude, and Nematocera becoming less abundant (Appendix One). Since the birds are spending a large amount of time foraging at or below 2 m altitude (Figure 2.4), the availability of Hemiptera used in the

calculation of selectivity may be over-estimated, and the proportion of Nematocera may be underestimated. However, neither of these effects would alter my conclusions. Since Nematocera were found to be selected against based on the 12 m sample, an underestimate of available Nematocera would only increase the degree to which Nematocera are selected against. Similarly, Hemiptera were found to be weakly selected for. If their availability had been overestimated, it would simply increase the estimate of the degree to which they are selected for.

<u>Changes in Selectivity with Nestling Age, Date of Sample, and Insect Abundance</u>

Nestling tree swallows grow from a mass of less than 2 g at hatching to a peak of up to 24 g before fledging (Chapter Five). Given the change in the energy demands of the brood associated with this growth, selection for large insects would be expected to be higher in older nestlings than in younger. In fact, insects selected by parents show relatively few changes over the course of development (Table 2.6). Diptera, including both the relatively small Nematocera and the Larger Brachycera, show slight proportional decreases with nestling age, but the only changes in size go counter to my expectations, with selection for insects < 3 mm increasing with age and selection for intermediate sized insects (5 - 7 mm) decreasing with age. Holroyd (1983) also found little change in nestling tree swallow diet with age, as did Kožená (1980) in the barn swallow (*Hirundo rustica*). The changes in selectivity that do occur with age may be partly explained by changes in selectivity associated with the progressing season, since changes

in selectivity for taxa with date show the same pattern as for changes with age (Table 2.7).

Insect abundances change dramatically from day to day (Figure 2.1), and these changes affect the reproductive success of the swallows (Chapters Six and Seven). Since obtaining the necessary food is easier when food is abundant, I predicted that tree swallow selectivities should increase with increases in insect abundance (J. M. Emlen 1966, MacArthur and Pianka 1966, Pulliam 1974). In general this expectation is not met (Table 2.6). Selectivity for the largest insects does increase slightly with increasing insect abundance, but there is no associated decrease in selectivity for very small insects.

The lack of change in selectivity with abundance of food seems to suggest that there are few time or energy costs associated with pursuit and handling of individual prey items. Thus, even though the foraging mode used by tree swallows (i.e. continual flight) is energy intensive (Williams 1988), once the decision to forage has been made, it becomes cost-effective to take smaller, presumably less profitable prey items, and is consistent with the possibility that the mechanism behind the observed selectivity is the different apparency of prey of different sizes (cf Li et al. 1985). Prey availability may influence selectivity on larger spatial or temporal scales, or may influence the decision to forage or not, but it does not seem to influence prey choice. In contrast, Quinney and Ankney (1985) concluded that tree swallows were more selective at sites where food was abundant. However, in determining the profitability of prey, Quinney and Ankney assumed that insects occur in patches of uniform sized individuals, and that more abundant (i.e. smaller) insects formed larger patches. Using

these assumptions, small, abundant insects (2-5 mm) were considered the most profitable because they occured in the largest patches. My observations of tree swallow foraging showed no evidence of a reliance on relatively dense patches of insects while feeding nestlings; tree swallows were observed to cover areas much larger than a single insect swarm and to return with a heterogeneous assortment of insect sizes and taxa after most foraging bouts. Therefore, I have ranked prey based on biomass alone and assumed that swallows are making choices based on individual items, not on patch quality. My analysis of Quinney and Ankney's data (1985; Table 2.7) suggests that selectivity for large insects was not higher where insects were more abundant (i.e., their Sewage site), although selectivity there for small and medium sized insects was higher.

All studies of tree swallows indicate that they select a distribution of food items that is skewed towards larger insects than the distribution of available insects (Table 2.7). This pattern is universal among studies of foraging in other species of swallows (Bryant 1973; Hespenheide 1975; Holroyd 1972, 1983; Turner 1982a, 1982b, 1983; Dyrcz 1984) and in insectivorous birds in general (e.g. Gibb and Betts 1963, Hespenheide 1971). Selection for taxa of insects used is also similar among these studies, with the exception of Quinney and Ankney's (1985) Backus field site, where Brachycera are preferred much more than at other sites and Hemiptera less so. Other reports of tree swallow diets from studies that have not measured insect availability show a range of diet composition similar to that reported here and in Table 2.7 (Beal 1918, Holroyd 1972, Blancher et al. 1987, Acosta and Mugica 1990, Blancher and McNicol 1991).

Table 2.7. Probabilities of selection for insect taxa and sizes in tree swallow diets for different studies of tree swallow diets. Standardized selection probabilities, B_i , given, based on equation 4.22 of Manly et al. (1993). Note that these equations give slightly different values for Ithaca than does equation 4.10 used in Table 2.5. See text for further details. Ithaca = Ithaca, NY, this study; Long Point = Long Point Ontario, Holroyd 1983; Backus = Backus Field, Port Rowan, Ontario, Quinney and Ankney 1985; Sewage = Sewage Lagoon, Port Rowan, Ontario, Quinney and Ankney 1985. Note that Backus and Sewage sites use different size categories.

Size	Ithaca	Long Point	Size	Backus	<u>Sewage</u>
0 - 3	0.011	0.047	1 - 3	0.027	0.098
3 - 5	0.166	0.050	4 - 6	0.193	0.351
5 - 7	0.172	0.155			
7 - 9	0.294	0.128	7 - 10	0.780	0.551
9 +	0.358	0.620			
<u>Taxa</u>					
Nematocera	0.185	0.200		0.161	0.211
Brachycera	0.386	0.175		0.629	0.215
Hemiptera	0.292	0.389		0.090	0.359
Other	0.137	0.236		0.120	0.215

The aspects of tree swallow foraging ecology measured here show little variability due to fluctuations in environmental conditions during the nestling period. Although the environment varies both spatially and temporally, consistent patterns in prey choice and site use are found, and, by integrating information from a variety of scales, a general pattern of resource use during the nestling period emerges. Tree swallows generally forage close to their nest sites, and concentrate on the area below 20 m altitude where insects are most abundant. Although their diet presents a broad range of the insects available in the air column, strong preferences for larger insects are found. The following chapter will examine other aspects of foraging ecology and the possible fitness consequences of variation in foraging behavior.

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CHAPTER THREE:

Foraging Ecology of Tree Swallows: Feeding Rates, Load Size, and Consequences of Variation in Foraging Patterns.

INTRODUCTION

Food is thought to be an important limiting factor on populations and distributions of birds (Lack 1954; Martin 1986, 1987; Safina et al 1988; Monaghan et al 1989; Rodenhouse and Holmes 1992), and patterns of variation among individuals may be linked to differences in reproductive success and survival (Pierotti and Annett 1987, Weathers and Sullivan 1989, Wunderle 1991). If food is a limiting factor in the ecology of birds, such a limit would likely be manifested in the ability of parents to deliver food to their altricial young (Lack 1954, 1968; Drent and Daan 1980, Williams 1988). In this chapter I describe patterns of food delivery of tree swallows (Tachycineta bicolor) feeding dependent offspring, and provide evidence showing a correlation between changes in foraging ecology and reproductive success. I measured two components of rate of food delivery, load size and feeding frequency, and present two estimates of the total food delivered by parents feeding a typical brood. I also examine differences between males and females in food delivery. Finally, I examine the possible effects of variation in foraging site use (Chapter Two) on two characteristics linked to fitness; nestling growth rate and parental nest defense.

METHODS

General Methods and Study Site

Tree swallows breeding in nest-boxes were studied at two sites near Ithaca, New York (42° 30' N, 76° 27' W). These sites are part of the Cornell

University Experimental Ponds Facility; both consist of large, flat, open, grassy areas with regularly spaced man-made ponds and a large, marshy lake. The sites are surrounded by forest and abandoned farm fields. Unit One is a 13-ha site with 41, 0.1-ha ponds and a 6-ha lake. There are 105 nest-boxes at this site, spaced 20 m apart. Unit One was used by 55 - 75 pairs of tree swallows between 1989 and 1993. Unit Two is a 20-ha site with 50 0.1-ha ponds and a 7-ha lake. Starting in 1990, 10 nest boxes were erected at Unit Two, each spaced 40 m apart. In 1991 and 1992 there were 22 boxes available, and 27 boxes were available in 1993. Breeding pairs ranged from 10 in 1990 and 1991 to 23 pairs in 1993.

Rate of Food Delivery

The rate of food delivery to nestlings has two components; 1) the number of visits made by the parents, and 2) the amount of food delivered on each visit (load size). Load size was determined from samples of food delivered by adult tree swallows to their nestlings (Chapter Two). The number of insects found in a bolus was converted to dry mass using the conversions in Table 2.1.

Visitation rate was measured using information from focal nest observations conducted in 1990 through 1992. Observation periods lasted fifteen to sixty minutes. Calculations of visitation rate by sex include only those observations where the sex of the visiting parent was known. Comparisons between Ponds Units are based on breeding pairs as the unit of analysis, and all observations are included.

Tests of Effects of Foraging Site Use

I tested two predictions about the influence of the use of foraging site on fitness by comparing swallows breeding at Unit One to those at Unit Two. The use of foraging sites was different at the two Ponds Units (Chapter Two), and I predicted that parents that spend more time foraging close to their nest should have nestlings with higher growth rates, because of lower travel times associated with foraging. This prediction was tested by comparing average nestling mass on day 12 for broods from Unit One with broods from Unit Two. Nestlings were weighed in 1990 - 1993. ANOVA of nestling mass in relation to year and Ponds Unit showed that year did not have a significant effect on nestling mass so data from all years were pooled. ANCOVA of nestling mass was used to compare nestling masses at Unit One and Unit Two, with brood size and hatch day included as covariates.

The second prediction I tested is that parents that spend more time foraging close to their nest should be able to respond to a perceived threat to their nest faster than parents foraging further from their nest. This prediction was tested by comparing the time it took for parents at each Ponds Unit to defend against the presence of a threat to their nest. Tree swallows vigorously defend their nests from potential predators, including tree swallow researchers (Winkler 1991, 1992). Nests were tested between nestling days 10 and 12. Nests at both units were tested on the same day when there were nests of the appropriate age at both units; no nest was tested more than once. Trials were conducted between 1300 h and 1700 h. For each test, I drove a car to within 10 meters of the nest, started a stopwatch, and ran to the nest-box. Upon reaching the nest a red sock was

stuffed in the nest hole and I placed one hand on the top of the nest box. The time it took for a parent to first be observed circling me or uttering an alarm was defined as the response time. If one or both parents were present and circling when I got out of the car, the response time was recorded as 0 seconds. The time it took for a parent to first dive at me was defined as the time to attack (Winkler 1992). If neither parent attacked within one minute of first response, the trial ended and no time to attack was recorded. In those trials where one or both parents attacked, the number of dives was counted for one minute after the first dive, yielding an "intensity of attack" in dives/minute. Comparisons of the defense behavior of swallows at the two sites were made using non-parametric tests.

RESULTS

Rate of Food Delivery

Food boluses contained an average of 18.1 insects and averaged 24 mg. Sizes of boluses were similar among years, except for 1991, when food boluses were significantly larger than in any other year (Table 3.1). However, little effort was invested in obtaining samples in that year, and it is likely that the samples that were obtained were skewed towards samples with many insects. Based on these data, the average dry mass of an insect in the diet is 1.33 mg, or approximately 750 dry insects per gram.

Males and females collected equally large boluses of insects, both in terms of mass and number of items delivered (Table 3.2). An F-test of the variance of load size found that the difference in variance between males

Table 3.1. Load size of tree swallows feeding nestlings. n= number of samples analyzed for each year. Mass in mg. Number of items per bolus and mass of bolus were significantly higher in 1991 than in the other years (ANOVA p < 0.001, Fisher PLSD for pairwise comparisons). Load size does not change with date ($R^2 = 0.003$, n = 213, p = 0.40), nestling age ($R^2 < 0.001$, n = 206, p = 0.92), or insect abundance ($R^2 < 0.001$, n = 214, p = 0.99).

Year	Ite	ms	Mas	s	n
	mean	se	mean	se	
1989	20.8	4.9	22.5	3.1	41
1990	12.4	2.0	22.7	2.3	7 8
1991	57.1	11.0	100.8	18.0	12
1992	16.1	3.1	20.8	3.3	63
1993	17.3	5.9	22.8	5.0	21

Table 3.2. Comparison of the size of food boluses delivered by males versus females. Samples from all years combined, n= number of samples, items = number of food items / bolus, mass = total mass of bolus in mg. Differences in number of items and mass were not significantly different (ANOVA p=0.853 for number of items, p=0.477 for mass).

Sex	Mean Items	se Items	Mean Mass	se Mass	n
Male	19.0	2.8	28.6	3.4	91
Female	18.3	2.4	25.3	3.1	107

and females was not significant (number of items F = 1.16, bolus mass F = 1.06, p > 0.10). Feeding rate was significantly higher for females than for males at both Ponds Units (Table 3.3).

The number of items delivered per trip was significantly higher at Unit One than it was at Unit Two (Table 3.4). Bolus mass did not differ significantly between sites. The average size of items delivered tended to be higher at Unit Two than it was at Unit One, but this difference was not significant (Table 3.4). Feeding rate did not differ between Ponds Units (Table 3.5).

Estimates of Total Feeding Rate

These estimates of food delivery can be used to calculate the rate at which adults feed nestlings. Since parents make more trips to the nest as nestlings age, the data in Table 3.5 were restricted to nestlings on day 10 or older, giving a mean visitation rate of 23 trips/hour (see also Winkler 1991). Load size was not found to vary with nestling age (McCarty unpubl.). Multiplying visitation rate (based on 15 hours of feeding per day) by mean bolus size gives an estimate of 6210 insects or 8625 mg of dry insects per day (Figure 3.1). An independent estimate of food required can also be derived from the energy requirements of nestlings. Assuming a brood size of five nestlings, this approach estimates a requirement of 7156 insects or 11000 mg of dry insects per day (Figure 3.1).

Table 3.3. Comparison of the feeding rates of males and females. Includes only observations where the sex of the feeding parent was known. Observations from all years combined. Percent visits = mean percent of total visits to each nest made by male or female, n = number of observation periods, se = standard error of mean percent). Difference in visitation rate between the sexes is significant (paired t-test, t = 2.3. p = 0.030), but differences between Ponds Units is not significant (ANOVA F = 0.03, p = 0.860).

Market Control of the	Percent visits by males	Percent visits by females	n	se
Unit One	38.1	61.9	31	6.4
Unit Two	36.1	63.9	15	10.7

Table 3.4. Comparison of the size of food boluses delivered by pairs at Unit One and Unit Two. Samples from all years combined, mean number of food items per bolus, bolus mass, and dry mass per item (standard error of mean). All masses in mg. n = number of samples. Number of items is significantly different (ANOVA F = 8.01, p = 0.005). Differences in bolus mass and mass per item are not significant (ANOVA F = 3.28, p = 0.070 for bolus mass, F = 2.59, p = 0.110 for mass per item).

	Number of items	Bolus mass	Mass per item	n
Unit One	20.2 (2.0)	25.3 (1.8)	4.8 (0.7)	179
Unit Two	6.7 (2.0)	17.0 (3.6)	8.0 (2.4)	31

Comparison of Nestling Growth Rates

Between 1990 and 1993 I obtained day 12 weights on 91 broods of nestlings at Unit One and 37 Broods at Unit Two. Nestlings in broods at Unit Two had a higher average nestling mass (22.1 g \pm 0.3) than nestlings from broods at Unit One (21.0 g \pm 0.3). This difference is statistically significant (ANCOVA with brood size and hatch day as covariates, effect of Ponds Unit significant with p = 0.025). Growth of nestlings at other ages also differed between Ponds Units (Chapter Five).

Comparison of Nest Defense

Parents at Unit Two responded more quickly to a threat to the nest. The mean time to respond at Unit One was 13.5 seconds, while parents at Unit Two responded in a mean time of 7.0 seconds (Table 3.6, Mann-Whitney U-Test p = 0.033, corrected for ties). Eight pairs had response times of 0 seconds (three at Unit One and five at Unit Two). When these pairs are excluded, the difference in response time is still significant (Mann-Whitney U-Test p = 0.040, corrected for ties).

Parents at Unit Two were more likely to attack once they had responded to a threat (Contingency table df = 1, χ^2 = 7.769, p = 0.005). Of those parents that attacked, there was little difference between the two sites in time to initial attack. Parents at Unit One attacked 17.6 seconds after first arrival, and parents at Unit Two 15.2 seconds after first arrival (Table 3.6). This difference is not statistically significant (ANOVA df = 27, F = 0.304, p = 0.586). There was also no difference between the Units in the intensity of attack among those parents that attacked. At Unit One, attacking parents

dove at a rate of 13.9 dives/min, and at Unit Two, attacking parents dove at a rate of 13.2 dives/min (Table 3.6).

DISCUSSION

Adult tree swallows feed at a high rate throughout the nestling period, reaching a peak of over 20 visits per hour, and capturing over 6000 insects a day. The range in feeding rate observed at Ithaca is similar to that reported for other studies of tree swallow foraging rates (Leffelaar and Robertson 1986, Quinney 1986, Williams 1988, Lombardo 1991, Winkler 1991). Mean bolus mass in this study (25 - 28 mg, Table 3.2) was similar to the bolus mass of 28 mg reported by Quinney (1986). The relative contribution of males was lower than that of females, with males making less than 40 % of the feeding visits. This pattern is similar to that reported by Lombardo (1991) for tree swallows breeding on Long Island, New York, and to that found by Dunn and Robertson (1992) in Alberta. In contrast, several studies in Ontario have reported equal feeding rates by males and females (Leffelaar and Robertson 1986, Quinney 1986, Dunn and Robertson 1992). This difference may be related to the quality of foraging habitat available, with males decreasing their care when food becomes more abundant (Dunn and Robertson 1992). When they did visit, males and females did not differ in the average size of the bolus delivered to nestlings, suggesting that differences in visitation rate reflect a real difference in parental care and are not a reflection of males and females pursuing different foraging strategies.

Tree swallows breeding at the two different Units showed differences in the amount of time they spent foraging within sight of their nests (Chapter Two). I predicted that parents foraging close to their nest should

Table 3.5. Comparison of the visitation rate by pairs of tree swallows at Unit One and Unit Two. Observations from all years combined, n= number of observations, se = standard error of mean feeding rate. Difference in feeding rate is not significant (ANOVA F=0.227, p=0.64).

	Feeds per hour	n	se	
Unit One	14.5	66	1.1	
Unit Two	15.5	33	1.9	

Table 3.6. Nest defense by tree swallow pairs at Unit One and Unit Two. Means (n, se) given for pairs at each Unit. See text for definitions. Mean response time is significantly different, (Mann-Whitney U-test, p = 0.033). Attack time and dives per minute are not different (Mann-Whitney U-test, p > 0.10).

	Response	Attack	Dives
	Time (sec.)	Time (sec.)	per min.
Unit One	13.5	17.6	13.9
	(24, 2.9)	(10, 3.8)	(10, 3.0)
Unit Two	7.0	15.2	13.2
	(22, 1.9)	(18, 2.4)	(18, 2.5)

Estimate of Food Delivered

Calculation of the amount of food delivered to a brood of tree swallow nestlings during the second half of the nestling period.

(23 feeds per hour)¹ (15 hours of activity)² = 345 feeds per day (18 insects per feed)³ 345 feeds = 6210 insects per day or (25 mg per feed)³ 345 feeds = 8625 mg per day

Estimate of Food Required

Calculation of the amount of food required for a brood of tree swallow nestlings during the second half of the nestling period.

Day 12 nestling metabolic rate⁴ = 48 kJ per day (48 kJ/day) 5 nestlings = 240 kJ/day/brood $(240 \text{ kJ/day/brood}) (21.8 \text{ kJ per gram of insects})^5$ = 11000 mg per day $(11000 \text{ mg/day}) (0.72 \text{ insects per mg})^3$ = 7920 insects per dayor $(11000 \text{ mg/day}) (25 \text{ mg insects per visit})^3$ = 440 feeds per day

Figure 3.1. Estimates of total food delivered to nestling tree swallows. Two independent estimates of food delivered are possible, the first based on observations of food delivery rates, the second based on nestling energetic requirements. ¹Feeding rate based on mean delivery rate to 38 nests on nestling day 10 and 11 (see also Winkler 1991). ² Appendix One. ³ Table 3.2. ⁴ Chapter Four. ⁵ Cummins and Wuycheck 1971.

be better able to defend their offspring from predators, and should be able to deliver food at a higher rate, resulting in faster growth. Nestlings at Unit Two did grow significantly faster than those at Unit One, with mean day 12 mass at Unit Two being over 1 g more than the mean mass at Unit One (see also Chapter Five). This result is especially striking since the food supply at Unit Two was actually slightly lower than that at Unit One (Appendix One). The prediction that feeding rate would be higher at Unit Two was not supported (Table 3.5), and the mass of the food bolus delivered by parents at Unit Two was slightly smaller than that of Unit One parents (although not significantly so; Table 3.4). It is possible that the tendency for parents at Unit Two to feed more frequently, although not significant, represents a real difference between the two groups. Additional foraging observations would be needed to address this hypothesis. A second alternative is that parents at Unit Two feed a higher quality diet to their nestlings. There is a non-significant trend towards parents at Unit Two feeding heavier items, and the diet at Unit Two contains more Odonates, the largest items in the tree swallow's diet (Appendix One). If these larger items are of higher quality, perhaps due to higher digestibility associated with relatively less chitin per gram, this difference could result in higher growth rates.

A second advantage of foraging close to the nest site is that the parents may be able to keep the nest in view and may be able to respond to threats to the nest more quickly than parents feeding further from the nest. The ability to respond quickly to threats could be an important determinant of fitness, since no level of defense will be effective if it comes after a predator has entered the nest cavity. As predicted, parents at Unit Two responded

faster to a perceived threat than did parents at Unit One. When parents did respond, they defended equally vigorously at each site, suggesting that the difference in response time was not due to fundamental differences between the defensive behavior or quality of parents at the two sites. This difference in response time is especially interesting given that parents at Unit One might be expected to gain an advantage in detecting threats because of the higher density of nesting swallows there and consequent vigilance of neighboring conspecifics (Winkler 1994).

Two differences between the two Ponds Units could result in the observed pattern. If insects were more abundant at Unit Two, the observation that parents spend more time foraging near the breeding site might be because it is a foraging hot-spot relative to the surrounding sites (Chapter Two). Swallows might then spend more time foraging near the nest. However, insect sampling suggests that insects are in fact less abundant at Unit Two (Appendix One). The habitat of surrounding areas was similar at the two Ponds Units and probably did not differ significantly in their insect fauna. The Ponds Units did differ, however, in the density of breeding swallows. During the seasons when these observations were made, breeding densities at Unit One were between 3 and 6 times the breeding densities at Unit Two. Because of the density of conspecifics, interference among foragers could decrease the profitability of foraging near the nest at Unit One, relative to Unit Two.

Although additional data will be necessary to conclusively identify the source of these differences between the Ponds Units, they do present a dramatic example of the importance of environmental variation occurring across a small spatial scale. The high rate of food delivery found, with each

adult capturing an average of one insect every 20 seconds, also suggests that even under conditions of relatively abundant food, the potential for small changes in foraging proficiency to result in differential fitness exists. In this way food can be a limiting factor in the ecology of birds, without a significant depletion in food resources. This will be especially true during the nestling phase of the breeding season, when demands on foraging parents are especially high.

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CHAPTER FOUR:

Changes in the Energetics of Thermoregulation with Age, Temperature, and Brood Size in Nestling Tree Swallows.

INTRODUCTION

An understanding of the ecological energetics of adult birds has been instrumental in increasing our understanding of the ecology of birds (i.e. Drent and Daan 1980, Root 1988, Paladino 1989). Although considerable work has been done on the energetics of adult birds, surprisingly little is known about the patterns of energy use of altricial nestling birds and how these patterns relate to the ecology and life histories of these birds (Weathers 1992). Raising offspring is an energetically demanding activity (Hails and Bryant 1979; Drent and Daan 1980; Westerterp and Drent 1985; Williams 1988), and in many species reproductive output may be limited by the amount of food the parents can deliver to the nest (Lack 1954; Ricklefs 1969; Martin 1987, 1992). An understanding of how nestlings use energy will be vital to understanding the patterns of reproduction seen in these birds. The pattern of energy use of nestlings is complicated by the fact that they are rapidly growing and developing through much of the nestling period. Associated with this growth and development is a shift from poikilothermy to homeothermy that has important implications for both the effect of ambient temperature on nestling energy requirements and the allocation of time by parents that must choose between feeding their offspring and providing heat directly to the nestlings by brooding. Finally, the importance of these factors are in turn influenced by brood size, which can mediate the effects of ambient temperature on nestlings by changing the thermal environment of nestlings and the age of effective

thermoregulation (Dunn 1979; O'Connor 1975a). Although these factors are known to be important in determining the energy budgets of nestlings, how these factors interact with each other and their relative importance to nestling energetics are not known.

Tree swallows (*Tachycineta bicolor*) are highly vulnerable to short-term fluctuations in environmental conditions during the breeding season, leading to reduced reproductive success (Chapter Six), a characteristic they share with other aerial insectivores (Lack and Lack 1951, Bryant 1975, Wrege and Emlen 1991). Because these fluctuations are important determinants of nestling survival, the ability of nestlings to cope with periods of reduced food supply and low ambient temperatures will be critical to the parents' reproductive success. In this chapter I present the results of a study exploring the effects of ontogenetic and environmental factors on the use of energy by nestling tree swallows. Specifically, I present data on the change in the cost of thermoregulation as nestlings grow, and use the statistical technique of path analysis to examine the relative influence of temperature, age, mass and brood size on metabolic rate and thermoregulation. I also address possible aspects of the life history and ecology of tree swallows that are influenced by these patterns of energy use.

METHODS

I monitored the nests of a population of tree swallows breeding at the Cornell University Experimental Ponds Facility, approximately 8 km north of Ithaca, New York. Nests were checked every other day beginning before egg laying and every day at the time of expected hatching to

determine the exact day of hatching. All nestlings used in this study were of known age.

Measurements of Metabolic Rate

In 1991, I measured the active-phase (i.e. day-time) resting metabolic rate (RMR) of nestling tree swallows on days 3, 6, 9, 12 and 16 (where day 1 = hatch day). Tree swallows normally fledge on day 21 and nestlings cannot be safely handled after day 16 because of the threat of premature fledging. RMR's of additional nestlings were measured at other ages, and those data were included in the path analysis described below. To measure metabolic rate, one or two nestlings from each nest were removed and held in a covered box where they were kept warm until they were transferred to the metabolic chamber. At least two nestlings remained in the nest so that the parents would not abandon the brood. Nestlings were tested twice at each temperature; once as brood members and once as individuals. Each nestling participated in no more than one trial of each combination of temperature and brood size. Broods consisted of five individuals of the same age tested at the same time, but were not necessarily from the same nest. Measurements of broods of three and four nestlings are included in the path analysis, making brood size a continuous variable. Nestlings were returned to their nests after testing. Although nestlings were gone from the nest for up to three hours, no mortality or other ill effects were observed to be associated with this procedure.

Oxygen consumption (VO₂) of nestlings was measured using closed chamber respirometry (Bennett 1986; Vleck 1987). Metabolic chambers were constructed from 1.9 liter paint cans. The insides of the cans were

painted flat black to minimize complications due to reflectance of radiant energy (Porter 1969). Although measurements were made during the nestlings active phase, darkened chambers were used to minimize activity within the chambers. Water vapor and CO2 were absorbed in the chamber using Drierite and KOH pellets respectively (Obst et al. 1987). Nestling metabolic rate was measured at 20°C and 30°C. Metabolic chambers were placed in a constant temperature cabinet, and metabolic chamber temperature was monitored with a type-T thermocouple attached to the inside wall. Nestling body temperatures were measured before and after each trial by inserting a type-T thermocouple into the proventriculus, and reading the temperature using an Omega HH-25 Digital Thermometer (Omega Engineering, Inc., Stamford, Connecticut) calibrated using an ice bath. To minimize the amount of time nestlings were away from the nest, I limited the acclimation period to ten minutes. A series of trials of two consecutive measures of resting metabolic rate showed no change in metabolic rate with a 20 to 30 minute acclimation period (n = 18, paired Ttest, p > 0.20), indicating that a ten minute period was sufficient. After the acclimation period, the chamber was sealed, and an initial air sample was taken. After 10 to 15 minutes, a second air sample was taken, and the chamber was ventilated.

The percent oxygen in each sample was measured using an Amatek N-22 Oxygen Sensor (Amatech, Inc. Pittsburgh, Pennsylvania) and an Amatek S-3A/1 Oxygen Analyzer. Constant flow rate through the sensor was maintained using a Harvard Apparatus Infusion Pump. In all cases the decrease in oxygen concentration was held to less than 1%. VO₂ was

calculated using equations from Vleck (1987) and converted to joules using a value of 20.08 J / ml O_2 (Williams and Prints, 1986).

The energetic cost of thermoregulation was determined for those nestlings and broods in which the same individual or brood was tested at both 20°C and 30°C on the same day. The energy cost of thermoregulation was defined as the scope for increasing metabolic rate, which is the ratio of the RMR at 20°C to the RMR at 30°C (Chappell et al. 1990). This definition provides an indication of the degree to which nestlings are expending energy for thermoregulation, above that required for maintenance. This results in a cost only in those nestlings that maintain their body temperature; in poikilothermic nestlings RMR at 20°C is lower than RMR at 30°C, and this index then represents the drop in RMR due to exposure to low ambient temperatures. The transition from energy savings to an energy cost associated with low ambient temperature makes this definition of thermoregulatory cost relevant to the discussion of ecology of nestling development. This definition reflects only energetic costs and savings; their will be other consequences of changing ambient temperature that are not reflected in this index.

Statistical Analyses

Data were analyzed using Mann-Whitney U-Tests to examine the effects of nestling age, brood size and ambient temperature on metabolic rate. In addition, the multivariate technique of path analysis was applied to the data to explore the interacting effects of five independent variables on metabolic rate. Path analysis was developed as a method for interpreting the causal relationships among sets of correlated variables,

and provides information on both the relative importance of the independent variables and an indication of the fit of the model to the data (Sokal and Rohlf 1981, Pedhazur 1982, Kingsolver and Schemske 1991), and has recently been applied to a variety of questions in ecology and evolution (Schemske and Horvitz 1988; Crespi and Bookstein 1989; Mitchell 1992, Wootton 1994). Path analysis allows the comparison of the relative effects of variables by comparing path coefficients (i.e. standardized partial regression coefficients), and gives an indication of the fit of the data to the model by examining the coefficient of non-determination, U_X . This coefficient is based on the multiple regression R2, and represents the sum of the effects of all unmeasured variables on the dependent variable. A basic introduction to path analysis is given by Pedhazur (1982), while Kingsolver and Schemske (1991) and Mitchell (1992) give a more specialized introduction to its use in ecology and evolutionary biology (see also Chapter Seven). In this case, I propose an a priori model of the causal relationships among five independent variables (ambient temperature, brood size, nestling age, nestling mass, and nestling body temperature) and the dependent variable of metabolic rate. In this model, all five independent variables are assumed to have a direct causal effect on metabolic rate. In addition nestling body temperature is affected by ambient temperature, brood size, nestling age and nestling mass, and nestling mass is influenced by nestling age. It is important to note that in path analysis these causal relationships are assumed to be correct, based on a priori knowledge of how these physiological and environmental variables will interact.

RESULTS

Metabolic rates of nestling tree swallows were influenced by both nestling age and ambient temperature. Metabolic rates of individual nestlings (Table 4.1) were significantly higher at 20°C than at 30°C for day 12 and 16 nestlings, but were significantly lower at 20°C for day 6 nestlings. There was no significant influence of temperature on metabolic rate in either day 3 or 9 nestlings. The pattern of metabolic rates for broods of 5 nestlings was similar to that for individuals (Table 4.2). Although differences were not statistically significant, day 3 and 6 broods had lower metabolic rates at 20°C than at 30°C, while day 12 broods had higher metabolic rates at 20°C than at 30°C. Sample sizes were small, and the danger of type II error is high, limiting the inferences that can be drawn from this result.

Nestling tree swallows grow rapidly, reaching adult mass of about twenty grams by day 11, after which mass decreases slightly (Chapter Five). At an ambient temperature of 20°C, the change in metabolic rate associated with nestling mass (Figure 4.1a) is described by the equation:

$$log (RMR) = 0.578 + 2.114 log (M)$$
 (4-1)

where RMR is measured as J *h-1, and M = mass in grams. This relationship explains a highly significant proportion of the variance in metabolic rate (R^2 =0.846, p < 0.001, n = 44). When ambient temperature is

30°C, the relationship between nestling metabolic rate and nestling mass (Figure 4.1b) is:

$$log (RMR) = 1.272 + 1.476 log (M)$$
 (4-2)

which again explains a large amount of the variance in metabolic rate (R^2 =0.922, p < 0.001, n = 52).

The cost of thermoregulation was strongly influenced by age (Tables 4.3 and 4.4). Day 3 and 6 nestlings do not regulate their body temperature and show a substantially lower metabolic rate at 20° C because of the associated drop in body temperature (Table 4.3). Day 9 nestlings are capable of some thermogenic response and show a similar metabolic rate at 20° C and 30° C even though body temperature is significantly lower at 20° C. Day 12 and 16 nestlings maintain their body temperatures above 35° C and show a true cost associated with thermoregulation. The same pattern is seen for broods of nestlings (Table 4.4). Broods showed a significant savings in the cost of thermoregulation over individual nestlings at day 16 (Mann-Whitney U-Test, p = 0.039), but there was no difference between individuals and broods in the cost of thermoregulation at other ages (Mann-Whitney U-Test, p > 0.10).

Path analysis of how ambient temperature, brood size, nestling age, nestling mass, and nestling body temperature, interact to influence metabolic rate shows that these five variables taken together explain a large percentage in the variation of metabolic rate (Figure 4.2, overall $R^2 = 0.822$, p < 0.001). Nestling age has only a small, non-significant direct effect on RMR, but a

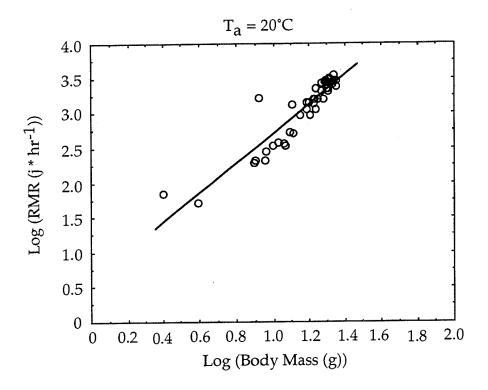
Table 4.1. Comparison of metabolic rates of individual nestling tree swallows at ambient temperatures of 20°C and 30°C. Age of nestlings in days and metabolic rate given as mean metabolic rate (n; se). p-values refer to results of Mann-Whitney U-Test comparing temperatures.

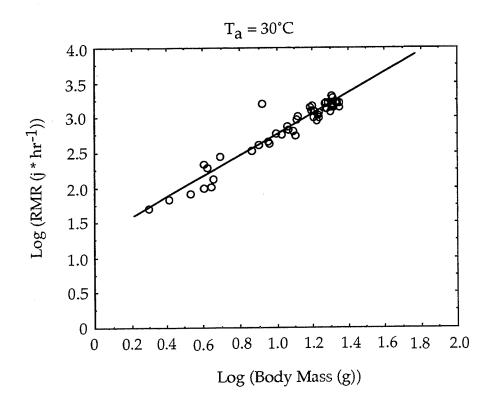
Age	<u>20°C</u> J * h ⁻¹	<u>30°C</u> J * h ⁻¹	p - value
3	61 (3; 10)	136 (9; 26)	0.157
6	425 (11; 114)	578 (11; 50)	0.010
9	1387 (10; 101)	1308 (9; 63)	0.807
12	2511 (8; 169)	1467 (9; 107)	0.002
16	2687 (8; 159)	1536 (8; 62)	0.001

Table 4.2. Comparison of chick-specific metabolic rates of nestling tree swallow broods at ambient temperatures of 20°C and 30°C. Age of broods in days and metabolic rate given as mean metabolic rate (n; se). p-values refer to results of Mann-Whitney U-Tests comparing temperatures.

Age	<u>20°C</u> J * h ⁻¹	<u>30°C</u> J * h ⁻¹	p - value
3	47 (2; 6)	149 (4; 11)	0.064
6	503 (2; 159)	592 (3; 113)	0.083
9	1170 (2; 11)	1171 (3;71)	0.833
12	2071 (2; 165)	1256 (3; 36)	0.083
16	1886 (3; 255)	1528 (3; 14)	0.513

Figure 4.1. The relationship between nestling mass and resting metabolic rate in tree swallows. Figure 4.1a shows the relationship between mass and metabolic rate at an ambient temperature of 20°C, while the relationship at an ambient temperature of 30°C is given in Figure 4.1b.





mean). Age is in days, n= number of swallows tested at each age, and $T_b=$ body temperature. "Cost" is the Table 4.3. Change in the cost of thermoregulation with age for nestling tree swallows. Each swallow was ratio of the rate of oxygen consumption at 20° C to the rate of oxygen consumption at 30° C. There is a tested once at 20° C and once at 30° C on the same day. Values given are means (standard error of the significant increase in the cost of thermoregulation with age (ANOVA, p = 0.0001).

Age n Mass (g) Tb 3 1 3.9 6 10 10.8 (0.6) 29.0 (0.5) 9 7 15.1 (1.2) 31.9 (0.8) 12 6 20.3 (0.8) 36.4 (0.8)	20°C	30°C	Ç	
1 3.9 10 10.8 (0.6) 7 15.1 (1.2) 6 20.3 (0.8)	Tb j*h-1*g-1	Tb	j*h-1*g-1	Cost
10 10.8 (0.6) 7 15.1 (1.2) 6 20.3 (0.8)	13.2		53.2	0.25
7 15.1 (1.2) 6 20.3 (0.8)	29.0 (0.5) 36.6 (7.3)	34.6 (0.6)	55.5 (2.7)	0.76 (0.18)
6 20.3 (0.8)	31.9 (0.8) 96.0 (18.2)	35.5 (0.8)	97.6 (16.6)	(60.0) 66.0
	36.4 (0.8) 123.4 (7.8)	37.8 (1.2)	75.8 (6.0)	1.66 (0.12)
16 6 21.0 (0.5) 38.1 (0.5)	38.1 (0.5) 125.9 (7.9)	38.5 (0.6)	72.0 (3.0)	. 1.75 (0.09)

0.0046). + = information available for only one of the two broods. * = Cost of thermoregulation significantly Table 4.4. Change in the cost of thermoregulation with age for nestling tree swallow broods. See Table 3 for lower for broods at age 16 days than for single nestlings at age 16 days (ANOVA F = 9.64, p = 0.017; Manndefinitions. Mass = average mass of per individual in each trial. Brood size equals 5, except for one brood Whitney U-Test, p = 0.039). Cost of thermoregulation does not differ between broods and single nestlings of three at age 6. There is a significant increase in the cost of thermoregulation with age (ANOVA, p = for other ages (p > 0.10, ANOVA, Mann- Whitney U-Test).

	Cost	0.36 (0.07)	0.76 (0.05)	1.06 (0.01)	1.61 (0.15)	1.23 (0.16) *
C	j*h-1*g-1	43.6 (2.6)	63.1 (8.5)	69.0 (0.2)	61.6 (0.8)	73.8 (0.5)
30°C	Tb		36.7 (0.8)	38.7 (0.5)	39.2 +	39.3 (0.8)
C	j*h-1*g-1	15.5 (1.9)	48.3 (9.7)	73.4 (0.7)	(6.2) 6.86	90.8 (11.5)
20°C	Tb		29.4 (0.1)	31.9 (0.1)	38.4 +	38.6 (0.4)
	Mass (g)	3.0 (0.0)	10.2 (1.3)	15.9 +	20.9 +	20.7 (0.3)
	и	2	2	2	7	8
	Age n	8	9	6	12	16

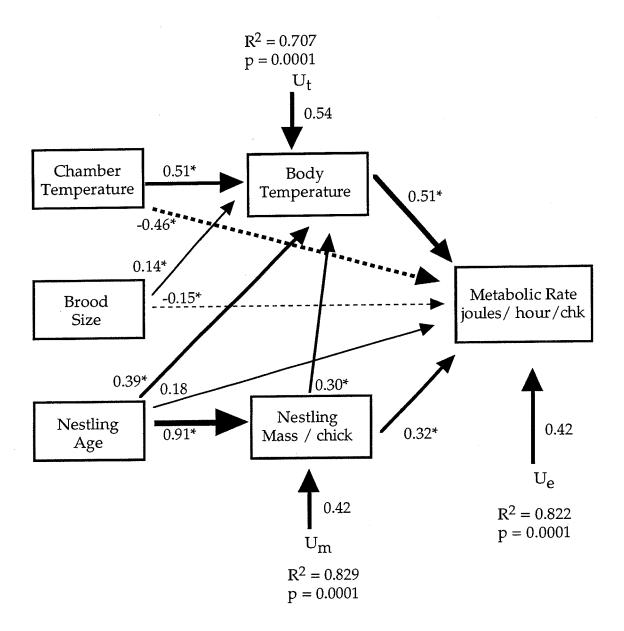


Figure 4.2. Path diagram showing the relationships between nestling metabolic rate and chamber temperature, brood size, nestling age, nestling mass, and nestling body temperature. The width of the arrows is proportional to the size of the path coefficient, with a dashed line indicating a negative effect and a solid line a positive effect. U_X is the coefficient of non-determination for variable x. Numbers next to the lines are the path coefficients; path coefficients marked with a " * " are significant at p < 0.05.

large indirect effect through nestling mass. However, there is a significant direct effect of age on body temperature, indicating that thermoregulatory ability increases with age, independent of body mass. Increase in brood size has a significant negative effect on metabolic rate, but brood size also has a positive effect on body temperature which acts to decrease the overall energy savings associated with brood size. Although this pattern is consistent across ages, the response of younger nestlings is expected to be more sensitive to the duration and magnitude of variation in ambient temperature (Chapter Six). Chamber temperature, body temperature, and nestling mass have strong direct and indirect effects on RMR. On the time scale used in this experiment, the overall effect of chamber temperature is reduced because it has a negative direct effect on RMR, countered by a positive, indirect effect through body temperature. However, the overall effect of nestling mass on RMR is enhanced because increases in mass are associated with a direct increase in RMR and an indirect increase in RMR through the effect of mass on body temperature.

DISCUSSION

Patterns of Energy Use

Energy use by nestling tree swallows increases rapidly as the nestlings grow and develop. It then levels off after the nestling's mass reaches its asymptotic level, following the pattern of other species that have been measured (Blem 1975, Williams and Nagy 1985, Mock et al 1991, Weathers and Sullivan 1991). The response of nestling tree swallows to ambient temperature also changes with age. The metabolic rates of young nestlings increase with increasing temperature in a manner typical of poikilotherms,

and after the nestlings become homeothermic, their metabolic rate decreases with increasing temperature, as has been found in other passerines (Dawson and Evans 1960, O'Connor 1975b, Mertens 1977, Marsh and Wickler 1982, Prinzinger and Siedle 1988).

Based on the allometric relationship between metabolic rate and body weight for adult passerines found by Lasiewski and Dawson (equation e; 1967) the predicted metabolic rate of tree swallows at asymptotic body mass (\approx 22 g) is approximately 1.42 kJ*h⁻¹; slightly lower than the metabolic rates of 1.47 kJ*h⁻¹ and 1.54 kJ*h⁻¹, for day 12 and 16 nestlings respectively, that were found here (Table 4.1, 30°C). These metabolic rates are similar to the daytime resting metabolic rate of 1.59 kJ * h⁻¹ for adult tree swallows, found by Williams (1988), suggesting that tree swallows in general have higher metabolic rates than other similarly sized passerines.

Path analysis shows that there are significant direct effects of chamber temperature, brood size, body temperature and nestling mass on nestling metabolic rates, and that these variables together explain a large percentage of the variability in nestling metabolic rate (Figure 4.2). Nestling age does not have a direct effect on metabolic rate but influences metabolic rate indirectly through its effect on nestling mass and body temperature.

<u>Thermoregulation</u>

The ability of altricial nestlings to maintain their body temperature is known to be influenced by the presence of brood mates (Dunn 1976, 1979; Clark 1982; Hill and Beaver 1982), nestling growth and mass (King and Farner 1961, Dunn 1975, Mertens 1977, Webb and King 1983), and other physical changes associated with nestling maturity (King and Farner 1961,

Clark 1982, Marsh and Wickler 1982, Ricklefs and Webb 1985, Choi et al. 1993). The relative importance of these factors in maintaining body temperature is not known. The results of the path analysis (Figure 4.2) in this study show that the ability to maintain body temperature is enhanced by increases in brood size, nestling age and nestling mass. Further, the path coefficients for these three factors suggest that, under laboratory conditions, nestling age and nestling mass are equally important in their contribution to the maintenance of body temperature, while the presence of brood mates has considerably less influence.

Several studies have indirectly estimated the cost of thermoregulation in nestling passerines by comparing resting and field metabolic rates and attributing the difference to the combined costs of activity and thermoregulation. Westerterp (1973) estimated that thermoregulation accounted for approximately 2 -8% of the metabolizable energy used by European starling nestlings (Sturnus vulgaris), while Weathers and Sullivan (1991) estimated that thermoregulation and activity combined accounted for about 33% of the total energy budget (which would represent approximately 1.8 x BMR in older nestlings) of yellow-eyed junco nestlings (Junco phaeonotus). Williams and Prints (1986) estimated that the combined cost of thermoregulation and activity was approximately 25% of the total budget (or up to approximately 1.6 x BMR just prior to fledging) in nestlings of the savannah sparrow (Passerculus sandwichensis). These estimates are based on different methods than those used in this study, and they do not distinguish between the costs of thermoregulation and activity, making direct comparisons to the present study difficult. However, the

estimates they found are within the range of values I found for individuals (up to $1.75 \times RMR$, Table 4.4) and broods (up to $1.23 \times RMR$, Table 4.5) of tree swallows.

Applying measures of the cost of thermoregulation to field studies is difficult, since the thermal environment of nestlings is unknown and probably highly variable both within and between nests. Measurements made under known, controlled conditions facilitate comparisons among species and studies by making the measurements less site and time specific. In addition, these measurements are independent of the activity costs included in previous measures of thermoregulatory costs. Although the temperatures used in this study (20°C and 30°C) are typical of air temperatures observed in natural tree swallow nests (McCarty unpubl. data), other characteristics of the thermal environment experienced by nestlings in the field are probably significantly different, making it necessary to exercise care in applying these results to field situations.

Brood Size

Brood size is known to influence the thermal relationship between altricial nestlings and the environment (Royama 1966; Mertens 1969; Dunn 1976, 1979; O'Connor 1975a; Bryant and Gardiner 1979). Many studies have shown that the age of effective homeothermy is reduced in broods compared to individual nestlings, and several studies have measured the energetic consequences of brood size. Westerterp et al (1982) measured food consumed by broods of nestling starlings (*Sturnus vulgaris*) and found that as brood size increased, food consumed per nestling decreased with no decrease in growth rate. O'Connor (1975a) measured the metabolic

rates of nestling blue tits (*Parus caeruleus*) and house sparrows (*Passer domesticus*) and found an energy savings associated with increasing brood size. Similarly, Hill and Beaver (1982) found differences between the metabolic rates of broods and individuals in red-winged blackbirds (*Agelaius phoeniceus*). Tree swallows show a similar savings, depending on age and ambient temperature (see also Dunn 1979 for the effects of brood size on nestling body temperature). In this study, no differences between broods and individuals were found at ambient temperature of 30°C, but day 16 nestlings at 20°C did have lower metabolic rates in broods compared to those tested alone (Table 4.1; Mann-Whitney U-Test, p = 0.041). This difference translates into a significantly lower cost of thermoregulation in day 16 nestlings (Tables 4 and 5; Mann-Whitney U-Test, p = 0.039).

The savings in the cost of thermoregulation found in older tree swallow nestlings may contribute to patterns seen in the length of the nestling period in different groups of birds. Tree swallows have a long nestling period for a passerine of their size (21 days), a characteristic they share with both other aerial insectivores and other cavity-nesting species (McCarty unpubl. data). Although cavity-nesting birds such as tree swallows are believed to have long nestling periods because their nests are relatively safe from predators (Lack 1948, 1968; von Haartman 1957) or because slowly developing chicks are somehow more buffered from food shortages than are rapidly developing chicks (reviewed by Ricklefs 1983), I suggest that there may be an additional benefit to a long nestling period because of the benefits of social thermoregulation (see also O'Connor 1984). If a brood of five, 16 day old tree swallows were to fledge and disperse they

would use approximately 13 400 J/h at 20°C (which is a typical ambient temperature during the nestling phase). By remaining together in the nest, those same nestlings use approximately 9400 J/h; a savings of 30% due to the thermoregulatory benefits of being in a brood. The actual savings are probably much higher since the nest also provides insulation and since leaving the nest necessarily increases the activity costs to nestlings. Consider a situation where available food supply decreases to a level where parents are able to deliver metabolizable energy at a rate of 8100 j/h. Based on the energy required for maintenance of old nestlings, parents with nestlings that have fledged and dispersed would be able to save 3 of their 5 offspring, assuming that fledglings do no foraging of their own. However, if the nestlings have not fledged, food delivery by the parents would be sufficient to save an average of 4.3 of their 5 offspring. This may be an important selective advantage in tree swallows where food supply varies dramatically from day to day and old offspring are at risk of starvation (Chapter Six). This benefit, together with the reduced cost of predation, could help explain the longer nestling period of cavity-nesting species.

Changes in nestling metabolic rate with age, temperature and brood size in tree swallows follow a pattern similar to that observed in other passerines. Path analysis shows that much of the variability in RMR can be explained by changes in ambient temperature, body temperature, brood size, brood age, and nestling mass. In addition, path analysis suggests that changes in nestling age and nestling mass contribute equally to the development of thermoregulatory ability. The energetic cost of thermoregulation is influenced by nestling age and brood size. It is

suggested that the cost of thermoregulation may be a significant factor in selecting for some aspects of avian life histories, such as the length of the nestling period.

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CHAPTER FIVE:

The Ecological Significance of Variation in Growth Rates of Nestling Tree Swallows

INTRODUCTION

In this chapter I examine the sources of variation in growth of nestling tree swallows (*Tachycineta bicolor*), examine the ecological significance of growth rate variation, and compare these patterns to other species of passerine birds. In addition, I compare the relative growth of body components that differ in their ecological significance. Several possible environmental parameters that might contribute to the variability in growth of tree swallows are investigated. In particular, I examine the significance of short-term periods of reduced feeding on growth and the possible long-term effects of these reductions.

Growth rates of nestlings influence the length of time offspring are dependent on their parents, their maximum energy requirement and rate of food delivery by the parents. Altricial birds are among the fastest growing vertebrates (Case 1978), with most small passerines attaining full adult mass within 10 - 20 days of hatching. The high rates of energy intake necessary to sustain such rapid growth accentuate the trade-offs that exist in attempting to optimize life histories within the context of the physiological constraints on growth (Lack 1968; Ricklefs 1969, 1973, 1984; O'Connor 1977b; Drent and Daan 1980; Sibly et al. 1985). Possible sources of selection on growth rates include predation rates on nestlings, changes in survival of parents, risk of starvation, and the timing of the onset of thermoregulation. In addition to selection on overall growth, the relative growth of different body components is also expected to vary in such a way as to maximize the probability of survival (Ricklefs 1979; Lilja 1983,

O'Connor 1984; Konarzewski et al. 1989, 1990). For example, organs devoted to processing of food, such as the gastrointestinal tract, should be large relative to body size in rapidly growing individuals, while organs devoted to locomotion will develop later.

Within a species, nestlings with below-average growth or size at fledging generally suffer from reduced post-fledging survival (Perrins 1965, 1988; Dhondt 1979; Garnett 1981; Nur 1984; Davies 1986; McGowan 1987; Gustafsson and Sutherland 1988; Tinbergen and Boerlijst 1990; Gebhardt-Heinrich and van Noordwijk 1991; Magrath 1991; Lindén et al. 1992, but see Ross and McLearn 1981, Nur and Clobert 1988, Sullivan 1989). Reduced growth may have a long-term effect on fitness, even when it does not appear to result in lower post-fledging survival, by decreasing the ability to obtain a breeding territory or mate or by lowering subsequent fecundity. For example, slow growth in nestling carrion crows (*Corvus corone corone*) results in smaller adults that are subordinate and less likely to become breeders (Richner 1989, 1992; Richner et al. 1989, see also Gustafsson and Sutherland 1988).

Previous studies have generally not differentiated between growth reductions due to chronic food shortages and those caused by short-term fluctuations in food supply. Several groups of birds with food supplies that are subject to short-term fluctuations, such as sea-birds (Hawksley 1957, Dunn 1975, Konarzewski and Taylor 1989) and aerial insectivores (Koskimies 1950; Lack and Lack 1951; Bryant 1978; Murphy 1983, 1985; Emlen et al. 1991; Wrege and Emlen 1991), are observed to undergo periods of interrupted growth and development, resuming normal growth once conditions improve. The long-term effects of these temporary growth

reductions have seldom been explored. Previous studies have found that nestlings subject to short-term shortages of food eventually attain full body mass (Wiggins 1990, Negro et al. 1994). Wiggins (1990) experimentally reduced the growth of nestling tree swallows by removing half the nestlings in a brood for several hours a day between days 5 and 8.

Nestlings receiving reduced food were found to be lighter and have shorter tarsi on day 9, but these differences disappeared by day 16. Wheelwright and Dorsey (1991) also found that tree swallow nestlings recovered from periods of slow growth before fledging. It is unclear whether such reductions in growth have a long-term effect on post-fledging survival.

I use three approaches to address the question of the ecological significance of growth rates: 1) I describe both the inter- and intra-specific variation in growth. Identifying factors important in producing variation is the first step in understanding the ecology of growth rates. 2) If growth and development are important constraints on the early life history of tree swallows, one would predict that energy and nutrients would be devoted to the development of those features most critical to young birds. The patterns of growth of several body components are described in this chapter to address what features show relatively fast or slow growth. 3) Finally, I examine the significance of short-term periods of reduced feeding on growth and the possible long-term effects of these reductions. Although the importance of chronic food shortages is well known, relatively little attention has been paid to short-term fluctuations in resources and their impact on subsequent aspects of an individual's biology. I present observational and experimental evidence to examine the importance of short-term reductions in growth.

METHODS

Tree swallows breeding in nest-boxes were studied at the Cornell University Experimental Ponds Facility (42° 30' N; 76° 27' W), near Ithaca, New York. This facility consists of two breeding sites located approximately 2 km apart. Unit One supported approximately 55 - 75 pairs of breeding tree swallows, and Unit Two had between 10 and 23 pairs. Swallows breeding at these sites are monitored closely for the exact date of hatching to determine nestling age. All nestling ages are given as hatch day = nestling day 1. Nestlings were weighed to the nearest 0.1g during the 1990 - 1993 breeding seasons using either Pesola spring scales or a portable O'Haus electronic balance. Lengths of the flattened and straightened wing chord (hereafter, wing chord), measured from the bend in the wing (carpal joint) to the tip of the longest primary, the 9th (outermost) primary, 1st (outermost) secondary, and 6th (outermost) rectrix were measured to the nearest 0.5 mm using a ruler with a wing and feather stop. Length of the tarsometatarsus (henceforth "tarsus") was measured to the nearest 0.1 mm using dial calipers. Disturbing nestlings after day 15 may cause premature fledging, so sample sizes for older nestlings are small and come primarily from nestlings removed for collecting or for metabolic rate measurements. Nestlings were measured at more than one age, but not every day, providing a mixed longitudinal sample (Ricklefs 1983). Logistic growth curves of the form:

$$M(x) = \frac{M(\infty)}{1 + \left[\frac{M(\infty) - M(0)}{M(0)}\right] e^{-Kx}}$$
 (5-1)

where x is the nestling age, M(x) is body mass at age x, M(0) is the initial mass, $M(\infty)$ is the asymptotic body mass, and K is the growth rate constant (Ricklefs 1983), were fitted using an iterative, least-squares procedure (nonlin module of SYSTAT; Wilkinson et al. 1992). All nestlings were banded with a numbered U.S. Fish and Wildlife Service band and a colored plastic band prior to fledging. Adult swallows were captured in mist nets prior to breeding or at their nest-boxes during breeding. Recaptures of banded birds provide a minimum estimate of survival, as birds which fail to return to the breeding site include individuals that disperse as well as those that die. I assume that the probability of dispersal is not influenced by pre-fledging growth and that recapture rate is highly correlated with survival (DeSteven 1980).

During June 1993, a sample of nestlings of known age were killed using CO₂ inhalation, weighed to the nearest 0.1 g using a portable electronic balance, sealed in plastic bags, and frozen until analysis. Nestlings were collected on nestling days 3, 6, 9, 12, and 15. At each age, all nestlings were taken from different broods; additional nestlings were taken from the same set of broods at subsequent ages.

Several fledglings of unknown age were collected in July 1993.

Although these individuals were not hatched from the main study colony, they were estimated to be between 30 and 50 days of age based on fledging dates of other nests in the area. Adults found dead near the study area were salvaged and assigned to either healthy or starved categories depending on the cause of death. Those adults killed by cars or predators were considered healthy at the time of death while those found dead in

nest-boxes during cold or wet weather were considered to have starved to death. Only those adults considered to be in good nutritional condition at the time of death are considered here.

At the time of analysis (August - December 1993), nestlings were reweighed and morphological measurements taken. All feathers were then removed, the carcass dissected, and stomach contents removed. Carcasses were divided into pectoralis muscles, heart muscle, gastro-intestinal tract, liver, remaining internal organs (kidney, testes/ovary, lungs), and the empty body (including skin). For some individuals the internal organs were treated as one component, resulting in different sample sizes (see Appendix Two for sample sizes). After the body components were weighed, all tissues were dried at 60 - 70 °C; water content was calculated from the mass loss during drying. Since it was necessary to pool body components to obtain a large enough sample for fat extractions, it was not possible to calculate water index (mass of water * lean dry mass-1) for each body component.

Growth rates of nestling tree swallows from this study were compared to published data on the growth of tree swallows from other sites and to the growth of other species of Hirundinidae. When not given in the original paper, latitude and longitude of the breeding sites were estimated from site descriptions. When not given, logistic growth rate constants were calculated for the mean population growth using equation 5-1.

To determine the importance of short-term reductions in growth to the subsequent growth of nestlings, a fasting experiment was conducted. Nests were paired to balance the experimental groups for nestling age, female age, clutch size and pre-treatment nestling mass. Within these pairs, nests were randomly assigned to either control or treatment groups. Initial mass was measured on day 5 and the morning of the start of the experiment (day 6). On the morning of day 6, nestlings were weighed between 0630 and 0730 h, and all of the nestlings from the experimental broods were removed and were fasted for one day. One or two nestlings from a non-experimental nest were placed in the treatment nests to keep the parents from abandoning while their chicks were gone. Nestlings in control broods were weighed and returned to the nest. Experimental broods were placed in controlled temperature chambers at either 20°C or 30°C under an incandescent lamp. When sufficient nests were available on a single day, triplets of nests were formed with a single unmanipulated nest acting as control for both a 20°C and a 30°C nest. Treatment nestlings were returned to the nest between 1730 and 1845 h. Control and treatment nestlings were weighed at the time the treatment broods were returned to their nests.

Nestlings in control and treatment nests were weighed between 1300 and 1800 h on nestling days 7, 8, 9, 10, and 12. Paired nests were weighed within one hour of each other. Wing chord of all nestlings was measured on days 10 and 12 and the tarsus was measured on day 12. Masses and wing lengths were not measured on day 12 at four nests which were disturbed by other researchers on that day. Tarsus length was still measured on day 12 for those nests, since adult tarsus length is obtained before day 12 (see below). For statistical analyses, each brood was treated as an experimental unit and the mean masses (or wing chords or tarsus lengths) for the chicks within broods were compared using paired t-tests.

RESULTS

The growth of nestling tree swallows exhibits the classic sigmoidal curve found in other passerines (Figure 5.1). Nestlings typically reach the adult mass of approximately 20 grams by day 10, less than half way through the 21-day nestling period. Nestlings may continue to increase their mass for one to three days reaching a peak mass of around 22 g. During the period of this study the heaviest nestling reached 27.6 grams. Fitting these data to a logistic growth curve gives a growth rate constant, K = 0.50, and an asymptotic mass = 21.7 g.

Growth of structural features such as wing chord, feathers, and tarsus is more linear than the increase in mass (Figure 5.2). Tarsus length matures most rapidly, reaching the adult length of 12 mm between day 8 and 9. The other bony structure measured, manus length, also matures rapidly, reaching its adult length of 25 - 26 mm by day 9. Flight feathers (primaries, secondaries, and rectrices) first emerge on day 7. Growth of the flight feathers continues throughout the nestling period, with growth being completed some time after fledging (Figure 5.2a).

Changes in Body Composition

Analyses of the body components of tree swallows of different ages show a consistent reduction in the water content of tissues accompanied by differential growth rates of the various components (Appendix Two). The changes in wet masses of the bodies of nestlings with pectoralis muscles and internal organs removed parallels the growth in mass of nestlings as a whole, with adult mass reached by day 9 and maximum mass being several

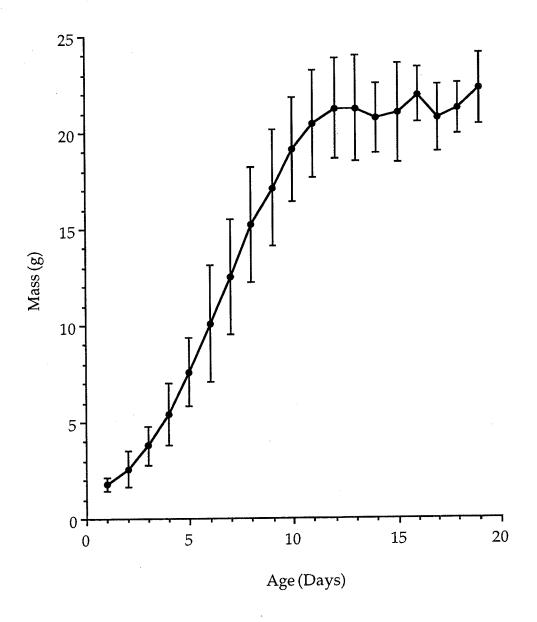


Figure 5.1. Increase in total mass during growth of nestling tree swallows at Ithaca, NY. Mean mass (± 1 st. dev.) based on measurements from Cornell Experimental Ponds Units One and Two, collected 1990 - 1993. See Appendix Two for sample sizes.

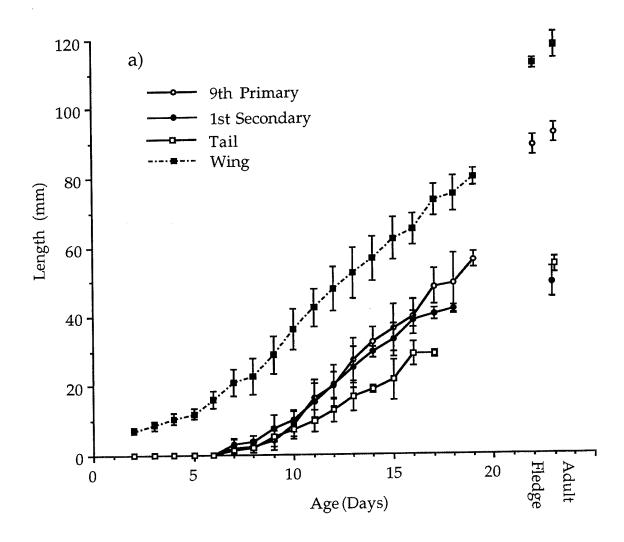
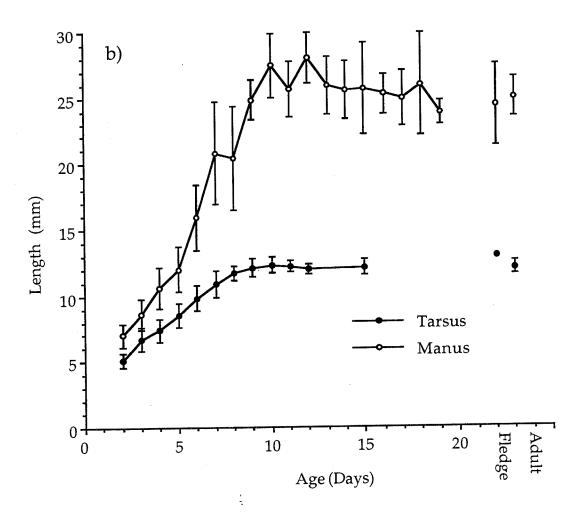


Figure 5.2. Growth of wing, flight feathers, manus, and tarsus of nestling tree swallows with analogous data for fledglings ("Fledge") and adults. Wing length and flight feathers (Figure 5.2a) measured in 1990 - 1993. Tarsus length (Figure 5.2b) measured in 1990 and 1993. Manus length (Figure 5.2b) calculated from difference between wing and 9th primary length.

Figure 5.2 (continued)



grams higher than that of adults (Figure 5.3a). However, because of the high water content of nestlings (Figure 5.3b) the dry mass of the empty bodies of nestlings is substantially lower than that of adults.

Between days 3 and 15, water content drops from 85 % to 69 %. The pectoralis muscles show a similar drop in water content, from 85 % at day 3 to 77 % at day 15 (Figure 5.4a). The mass of the pectoralis muscles increases steadily throughout the nestling period to a dry mass of 0.5 g by day 15, still substantially below the adult dry mass of 0.8 g (Figure 5.3b). The intermediate mass of the fledglings' pectoralis muscles suggests that full adult pectoral mass is not obtained until well after fledging.

The internal organs make up a larger percentage of the total mass of young swallows than of older swallows. Internal organs make up over 34 % of the dry mass of day 3 nestlings (Figure 5.3b). This falls to 23 % by day 15, and 18 % in adults. The absolute mass of the internal organs is also larger in older nestlings than in adults (Figure 5.3b). However, among the internal organs examined, this pattern varies. The liver and gastrointestinal tract are largely responsible for the overall pattern in growth of the internal organs, with both attaining dry masses in excess of those in adults by day 9 (Figure 5.4b). The heart muscle grows steadily throughout the period, making up approximately 1.5 % of the total dry mass of the body throughout the period. The pattern for the remaining organs (lungs, kidneys, and reproductive organs) shows that their relative masses increase throughout the nestling period but reach only half those of adults by day 15 (Figure 5.4b). The adult mass of this component is highly variable, due largely to the variability in the size of the reproductive organs through the pre-breeding and breeding seasons.

The allocation of biomass to various body components, as measured by the percent of the total dry mass accounted for by each component, also changes with age. The relative size of the internal organs decreases through the nestling period, from over 34 % of the total dry mass at day 3 to 22.5 % at day 15 (Figure 5.5a). Most of this difference is due to the decrease in the relative size of the gastrointestinal tract, which falls from 22 % to 13 % of the total dry body mass between day 3 and 15 (Figure 5.5b). The relative size of the heart remains constant throughout the nestling period, at 1.4 % of the dry mass (Figure 5.5b). Conversely, the relative size of the pectoralis muscle increases steadily as nestlings age, from 1.3 % on day 3 to 8 % on day 15 and 12 % in fledglings (Figure 5.5a).

Post-Fledging Survival

Nestling growth was significantly related to the probability that a nestling would be recaptured at Unit One, either as a spring migrant or a breeding individual. Nestling mass and wing were measured at different ages in different years. For comparisons among years, measurements were standardized by subtracting the mean value for each year from each individual's mass or wing length and then dividing by the standard deviation for that year, to produce a mean of 0 and standard deviation of 1 for each year's measurements. Data from 1989 - 1993 were then pooled. The pooled data show that nestlings that were subsequently recaptured were heavier and had longer wings than did nestlings that were not recaptured (Table 5.1). Trends for each year taken separately were similar, although not all were significant (McCarty unpublished). Tarsus length was measured in 1989 only, and the same pattern was found, with

Figure 5.3. Wet and dry masses of the major body components of tree swallows during nestling growth and for fledglings ("Fledge") and adults. Regressions of body components on age for wet mass (Figure 5.3a): total body, $R^2 = 0.931$, y-intercept = 0.75, coeff. = 1.63, p < 0.001; empty body, $R^2 = 0.875$, y-intercept = 0.70, coeff. = 0.96, p < 0.001; pectoralis, $R^2 = 0.917$, y-intercept = -0.53, coeff. = 0.16, p < 0.001; internal organs, $R^2 = 0.859$, y-intercept = 0.34, coeff. = 0.34, p < 0.001. Regressions of body components on age for dry mass (Figure 5.3b): total body, $R^2 = 0.968$, y-intercept = -0.62, coeff. = 0.45, p < 0.001; empty body, $R^2 = 0.967$, y-intercept = -0.48, coeff. = 0.32, p < 0.001; pectoralis, $R^2 = 0.899$, y-intercept = -0.13, coeff. = 0.04, p < 0.001; internal organs, $R^2 = 0.898$, y-intercept = -0.01, coeff. = 0.10, p < 0.001.

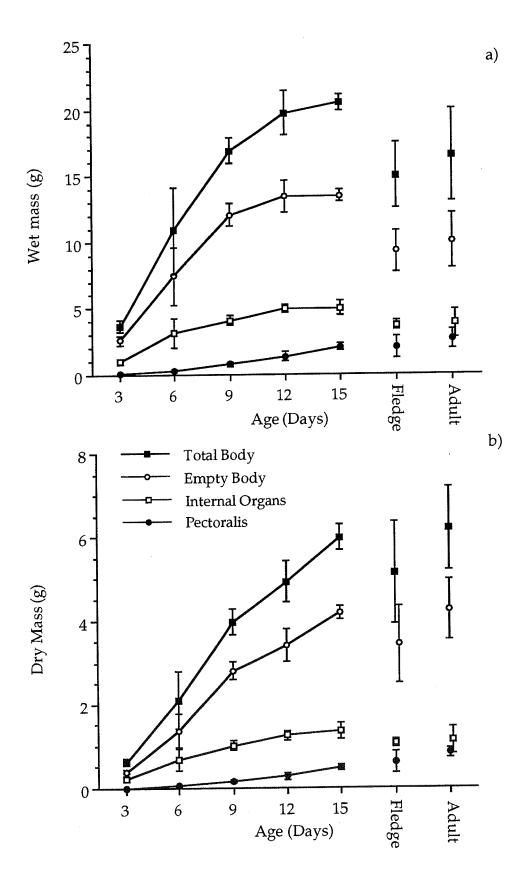
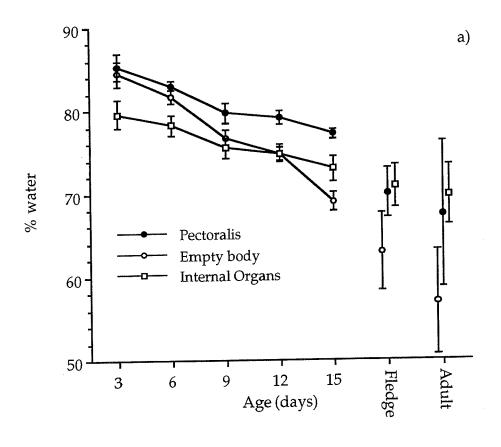


Figure 5.4. Water content of the major body components and dry masses of internal organs of tree swallows. Regressions of water content on age (Figure 5.4a): empty body, $R^2 = 0.954$, y-intercept = 0.89, coeff. = -0.01, p < 0.001; pectoralis, $R^2 = 0.894$, y-intercept = 0.87, coeff. = -0.01, p < 0.001; internal organs, $R^2 = 0.798$, y-intercept = 0.81, coeff. = -0.01, p < 0.001. Regressions of dry mass of internal organs on age (Figure 5.4b): liver, $R^2 = 0.792$, y-intercept = 0.00, coeff. = 0.03, p < 0.001; heart, $R^2 = 0.815$, y-intercept = -0.01, coeff. = 0.01, p < 0.001; GI tract, $R^2 = 0.852$, y-intercept = 0.02, coeff. = 0.05, p < 0.001; other organs, $R^2 = 0.886$, y-intercept = -0.01, coeff. = 0.01, p < 0.001. Data on masses of individual organs was not collected for fledglings.



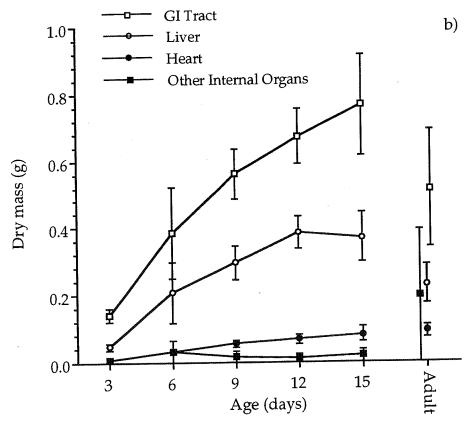
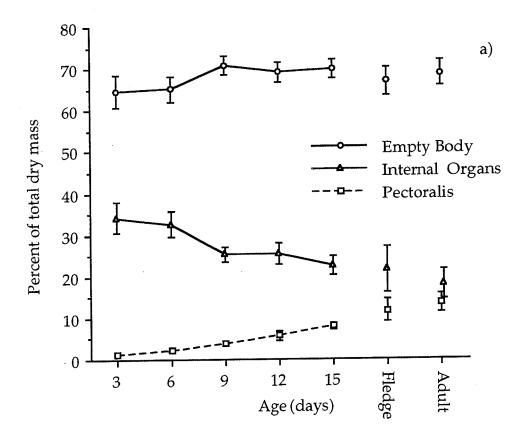
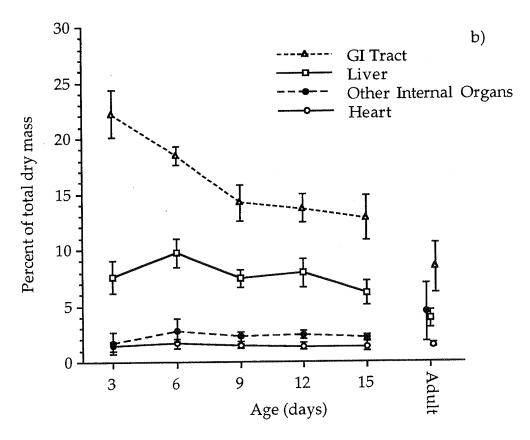


Figure 5.5. Percent of total dry mass for individual body components of tree swallows. Regressions of major body components on age (Figure 5.5a): empty body, $R^2 = 0.349$, y-intercept = 0.64, coeff. = 0.00, p < 0.001; pectoralis, $R^2 = 0.922$, y-intercept = -0.01, coeff. = 0.01, p < 0.001; internal organs, $R^2 = 0.731$, y-intercept = 0.37, coeff. = -0.01, p < 0.001. Regressions of internal organs on age (Figure 5.5b): liver, $R^2 = 0.136$, y-intercept = 0.09, coeff. = 0.00, p = 0.65; GI tract, $R^2 = 0.784$, y-intercept = 0.24, coeff. = -0.01, p < 0.001; other organs, $R^2 = 0.062$, y-intercept = 0.02, coeff. = 0.00, p = 0.183.





nestlings that were recaptured having longer tarsi than those that were not recaptured (Table 5.1).

Variability in Tree Swallow Growth Rates

Nestling growth rates varied with breeding location, year, and hatch date. The growth of swallows breeding near Ithaca lies within the range of variability seen in six other published studies (Figure 5.6). Values for the growth rate constants vary between K = 0.42 (Marsh 1980) to K = 0.59 (Zach and Mayoh 1982), with an average K for the six studies of 0.51 (standard deviation = 0.06). No pattern of nestling size with location was seen in these data (Figure 5.7), indicating that the differences observed in Figure 5.6 are due to local habitat effects, not clinal variation. Similar patterns are seen when day 10, day 12, maximum, and asymptotic mass are used (McCarty unpublished). The differences between the two breeding sites at Ithaca support this. Although these sites are separated by only 2 km, growth was consistently higher at Unit Two (Figure 5.8), with K for Unit One = 0.49, and K for Unit Two = 0.53. Growth also varied among years of this study at the Ithaca study sites (Figure 5.9), with K varying from 0.49 in 1992 to 0.56 in 1991. This variation is also evident when masses at different ages are compared, rather than K coefficients. Both year and Ponds Unit have significant effects on nestling mass on days 4 through 10 (Two factor ANOVA, Table 5.2). For day 12 nestlings, year is no longer significant, although Ponds Unit and the interaction between year and Ponds Unit remain significant (Table 5.2).

When replacement nests are excluded by eliminating nests hatching after 15 June, nestling mass at a given age tends to be weakly correlated with nestling hatch day (Table 5.3). The slopes of the regressions for nestlings younger than day 11 and for nestlings older than day 12 are positive, indicating that growth is faster later in the season and that asymptotic mass is also higher. Since tree swallow nestlings reach their peak mass about halfway through the nestling period and then show a slight decline in mass, the negative slopes for days 11 and 12 are probably the result of faster growing nestlings reaching peak mass at a slightly earlier age. The fast growing nestlings would then begin to decline in mass at the same age the slower growing nestlings are reaching their peak mass.

Comparison to other Species

Growth of nestling tree swallows was within the range of variability seen in the family Hirundinidae (Table 5.4). Ricklefs (1968a) provides growth constants for 54 species of small and medium-size passerines (excluding Hirundinidae and species with adult mass over 100 g) from 14 families or subfamilies. The average K for these passerines is 0.501 (standard deviation = 0.079), significantly higher than the mean for 10 species of Hirundinidae (mean K = 0.434, st. dev. = 0.07, t-test, t= 2.93, p = 0.017). Ricklefs (1968a) also provides the ratios of asymptotic mass to adult mass for 58 species of small and medium-size passerines (excluding Hirundinidae and species with adult mass over 100 g). Hirundinidae have a significantly higher ratio (mean = 1.13, st. dev. = 0.17) than do non-Hirundines (mean = 0.87, st. dev. = 0.12; t = 5.81, p < 0.001).

Table 5.1. Comparison of the size of nestlings that subsequently returned to the study site to those that were never recaptured. Mass and wing chord are standardized to a mean = 0.0 and standard deviation = 1.0 within each year and then pooled for all years where data are available. Mass data is from 1989-1993, wing data from 1989, 1990, 1992, and 1993. Tarsus lengths were collected for 1989 only so those data were not standardized. For each group, mean scores (and standard deviation, n) are given.

	Not Returned	Returned	ANOVA
Mass	-0.04	0.21	F = 11.56
(standardized)	(1.04, 1426)	(0.75, 215)	p = 0.007
Wing Chord	-0.03	0.19	F = 6.37
(standardized)	(1.01, 1083)	(1.01, 150)	p = 0.012
Tarsus length	12.21	12.50	F = 5.011
	(0.62, 192)	(0.43, 23)	p = 0.026

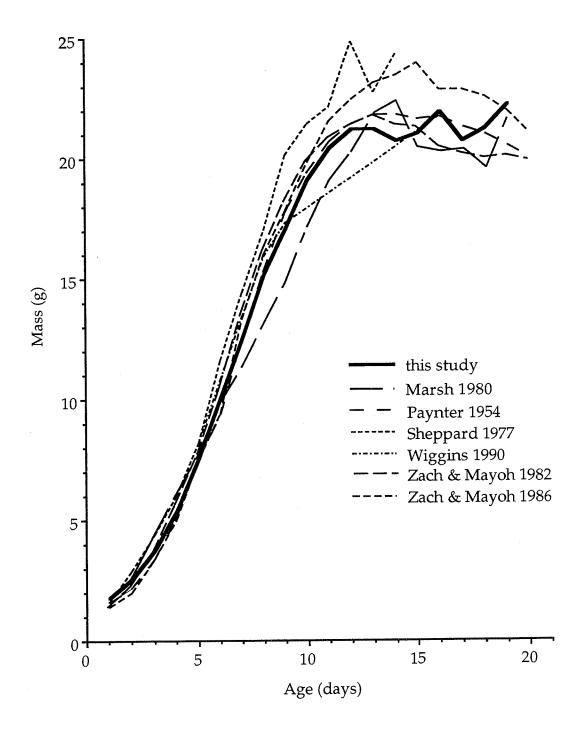
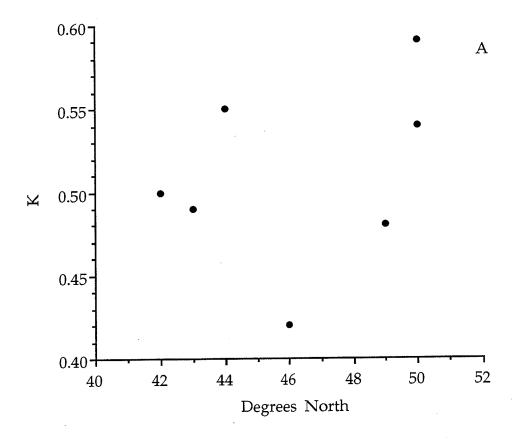
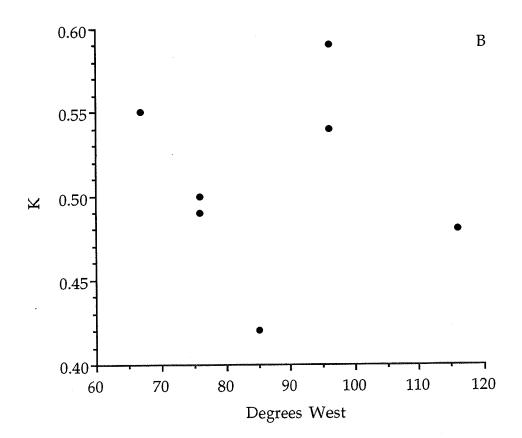


Figure 5.6. Variability in growth of nestling tree swallows from different locations. Data from: Paynter 1954 (New Brunswick); Sheppard 1977 (New York); Marsh 1980 (Michigan); Zach and Mayoh 1982, 1986 (Manitoba); Wiggins 1990 (British Columbia), this study (New York).

Figure 5.7. Change in nestling growth rate constant, K, with latitude and longitude. Multiple regression of growth constant, K, on latitude (Figure 5.7a) and longitude (Figure 5.7b) of nestling tree swallows; n=7, $R^2=0.37$, p=0.40. See Figure 5.6 for sources of data.





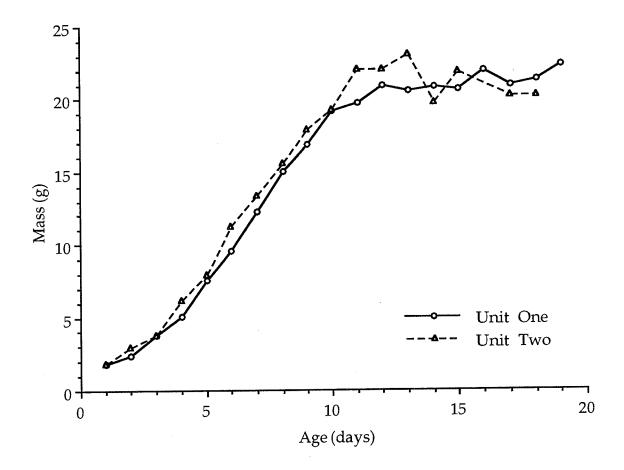


Figure 5.8. Comparison of growth of nestling tree swallows from Cornell Experimental Ponds, Unit 1 and Unit 2.

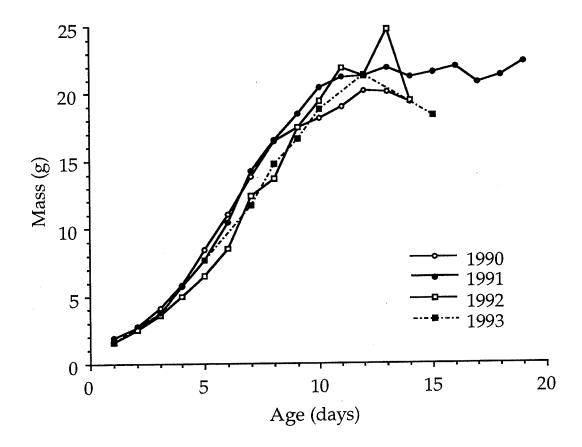


Figure 5.9. Variation in growth of Ithaca tree swallows among years. Pooled data from Cornell Experimental Ponds, Unit 1 and Unit 2.

Table 5.2. Two factor ANOVAs of nestling mass for Ithaca tree swallows for each age. Year is hatch year (1990 - 1993 except where noted), Ponds Unit is location of hatch, and Year x Unit is the interaction term from the ANOVA. p - values and (F - values) given for each variable. * 1993 excluded for lack of data. Underlined p-values denote significant effects after application of a sequential Bonferroni adjustment (Rice 1989) across ages.

Age	Year	Unit	Year x Unit
2*	0.695	0.065	0.117
	(0.365)	(3.451)	(2.169)
3	<u>0.0001</u>	0.837	<u>0.0001</u>
	(9.358)	(0.042)	(9.367)
4*	0.026	<u>0.0002</u>	<u>0.0001</u>
	(3.694)	(13.962)	(9.494)
5	<u>0.0001</u>	<u>0.0001</u>	<u>0.0001</u>
	(21.736)	(32.290)	(8.898)
6*	0.015	<u>0.0025</u>	0.031
	(4.281)	(9.384)	(3.537)
7	<u>0.0001</u>	<u>0.0001</u>	0.022
	(17.202)	(17.237)	(3.231)
8	<u>0.0001</u>	<u>0.0002</u>	<u>0.0001</u>
	(17.056)	(14.490)	(7.029)
9	<u>0.0001</u>	<u>0.0001</u>	<u>0.005</u>
	(10.665)	(23.041)	(4.290)
10	<u>0.0001</u>	0.019	<u>0.0001</u>
	(7.272)	(5.537)	(7.600)
12	0.567	<u>0.0001</u>	<u>0.006</u>
	(0.676)	(26.681)	(4.236)

Table 5.3. Regressions of nestling mass on hatch day, following the general form mass = intercept + (coeff.)(hatch day). Nests with hatch day after 15 June are excluded to eliminate replacement nests. Masses of nestlings on day 13 and older are pooled into the 13+ category. Underlined p-values denote significant relationships after application of a sequential Bonferroni adjustment (Rice 1989) across ages.

<u>Age</u>	Intercept	Coeff.	<u>R²</u>	p-value	n
1	1.68	0.00	0.00	0.84	286
2	0.06	0.08	0.06	0.001	165
3	2.02	0.05	0.04	0.0001	621
4	4.35	0.04	0.01	0.109	285
5	4.41	0.10	0.05	0.0001	554
6	-1.82	0.37	0.21	0.0001	166
7	7.62	0.15	0.05	0.0001	439
8	6.30	0.28	0.14	0.0001	502 ⁻
9	11.27	0.18	0.06	0.0001	628
10	17.07	0.06	0.01	0.014	656
11	27.15	-0.21	0.05	0.009	129
12	22.99	-0.05	0.07	0.07	605
13+	14.65	0.20	0.06	0.0014	166

Table 5.4. Comparison of the growth rates of swallows and martins, family Hirundinidae. Fledging and adult wing is wing chord in mm. Nestling period in days, masses in grams. K is the growth constant of the logisitic growth curve (see text).

Species	mass at hatching	fledging mass	fledging wing	adult mass	adult wing	nestling period	¥ .	sources
Progne subis	4.0+	47-51+		56	118.4	27-31	0.38-0.40	1,2,3,4
Progne chalybea	3+	36+		41.5	131.1	25-28	0.40	1,5
Progne tapera	4+	35+		36.1	127	28	0.28	1,5
Tachycineta bicolor	1.8	22.2	9.62	20.1	117.4	21.	0.49-0.56	1,2,6
Tachycineta thalassina	1.7	17.0		15	118.4	23	0.41	1,2,7
Stelgidopteryx serripennis	1.5+	15.0+	84+	15.9	107	18-21	0.46	1,2,8
Riparia riparia	1.5+	15.8†		13.5	107	22	0.41-0.58	1,9
Hirundo pyrrhonota	1.6-2.2	21.5		21.6	109	24	0.43-0.55	1,2,10
Hirundo rustica	1.9+	18.6+	91+	18.9	123.1	18-23	0.46-0.56	1,2,11
Hirundo tahitica	1.8+	14.6	76+	14.1	102+	19-21	0.42	12
Delichon urbica	1.7	17.7	100.6	18.3	111	27		13,14,15

1 = Turner and Rose 1989, 2 = Ricklefs 1968a, 3 = Ricklefs 1968b, 4 = Allen and Nice 1952, and Hill 1994, 5 = Turner 1984, 6 = McCarty this volume, 7 = Edson 1943, 8 = Lunk 1962, 9 = Petersen 1955, 10 = Stoner 1945, 11 = Jones 1987, 12 = Bryant and Hails 1983, 13 = O'Connor 1977a, 14 = Bryant and Gardiner 1979, 15 = Prinzinger and Siedle 1988. = estimated from figure

Effects of Short-Term Reductions in Growth

Nestlings were fasted on day 6 at either 20 °C or 30 °C. Although nestlings held at 30 °C lost more mass, the absolute mass of the two groups did not differ after day seven (30 °C = 10.7 ± 0.7 g, 20 °C = 10.4 ± 0.6 g, Anova df = 17, F= 0.074, p = 0.789). For the following analyses I have pooled the nestlings held at the two temperatures into a single experimental group. The effects of temperature in this experiment are discussed in detail in Chapter Six.

Control broods were paired with more than one treatment brood when triplets of nests were formed on a single day, consisting of a 20 °C, 30 °C, and a control nest. The experimental group contained a total of 18 broods, each of which was paired with one of 11 control broods. Initial mass of the control and treatment broods did not differ when measured on day 5 or when the nestlings were removed from the experimental nests the morning of day 6 (Table 5.5). There were no significant differences in brood size between experimental and control nests; broods consisted of either 4, 5, or 6 nestlings.

Experimental nestlings lost an average of 0.7 g per nestling during day 6, while control broods gained an average of 1.9 g per nestling during the same period. Nestlings in the experimental broods remained significantly lighter through day 10. On day 12 control nestlings were still heavier than experimental nestlings but the difference was no longer significant (Table 5.5). The experimental treatment also resulted in a difference in structural size, with both wing chord and tarsus length being smaller in 10 and 12 day experimental nestlings (Table 5.5).

Given the observed relationship between growth and postfledging survival in this population (Table 5.1), one would predict that nestlings with artificially reduced growth rates would return at a lower rate than unmanipulated nestlings. There was, however, no significant difference in return rates of nestlings from experimental and control broods (Figure 5.10). In fact, experimental nestlings returned at a higher rate than nestlings both from the control broods and from the population as a whole. Although this result suggests that the experimental manipulation did not impact nestling survival, among the experimental nestlings there is a significant relationship between the amount of mass lost during the manipulation and the proportion of the brood recaptured the following year (Figure 5.10).

Patterns of reduced growth similar to those observed in my starvation experiments can be seen in cases of natural starvation due to inclement weather. During a four-day period of low temperatures, rain, and reduced availability of insects, beginning on 19 June 1992, most adult tree swallows stopped feeding their nestlings. Although the majority of the nestlings died after three or four days (Chapter Six), some nestlings that hatched at the beginning of the period survived. These nestlings failed to grow or develop through this period, and, once feeding resumed on 23 June, they remained several days behind their normal growth trajectory (Figure 5.11). Although these nestlings fledged successfully, the reduced growth experienced does seem to have resulted in a long-term effect on those nestlings. Nestlings from the five nests that hatched during the period of adverse weather were less likely to be recaptured than nestlings

Table 5.5. Comparison of broods starved on day 6 to control broods. Values are means of the mean brood measurement (SE) for each treatment. N=18 broods. Masses in grams, wing and tarsus measured in mm. Paired, two-tail T-test. Underlined p-values denote significant differences after application of a sequential Bonferroni adjustment (Rice 1989) across ages.

	Control	Starved	df	T	p-value
Brood size	5.3 (0.2)	5.4 (0.2)	17	1.14	0.269
Day 5 mass	8.3 (0.8)	7.9 (0.3)	17	1.56	0.137
Day 6 mass (AM)	9.5 (0.3)	9.0 (0.3)	17	1.47	0.159
Day 6 mass (PM)	11.4 (0.3)	8.3 (0.3)	17	10.57	< <u>0.001</u>
Day 7 mass	13.5 (0.2)	10.6 (0.4)	17	9.65	< <u>0.001</u>
Day 8 mass	16.1 (0.3)	13.4 (0.5)	17	5.97	< <u>0.001</u>
Day 10 mass	19.9 (0.2)	18.4 (0.5)	17	3.84	0.001
Day 12 mass	22.1 (0.4)	21.7 (0.5)	13	0.72	0.482
Day 10 wing	36.0 (0.7)	32.8 (1.1)	17	3.29	<u>0.004</u>
Day 12 wing	50.0 (0.9)	46.7 (1.0)	13	3.11	<u>0.008</u>
Day 12 tarsus	12.1 (0.1)	11.9 (0.1)	17	4.77	< <u>0.001</u>

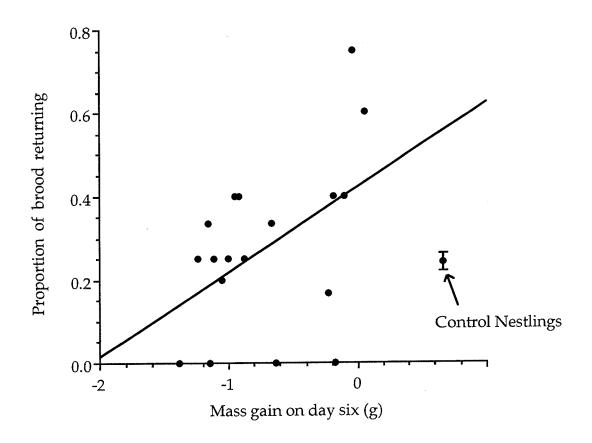


Figure 5.10. Post-fledging survival of nestlings from the starvation experiment. Percent survival of fasted and control nestlings did not differ (paired t-test, n=18, t=0.893, p=0.39). Among the fasted nestlings, those that lost less mass were more likely to return, with the line representing the least squares regression (n=18, regression $R^2=0.219$, F=4.499, p=0.0499). When broods that had no nestlings return are excluded, this relation is stronger (n=14, $R^2=0.383$, F=7.44, p=0.018).

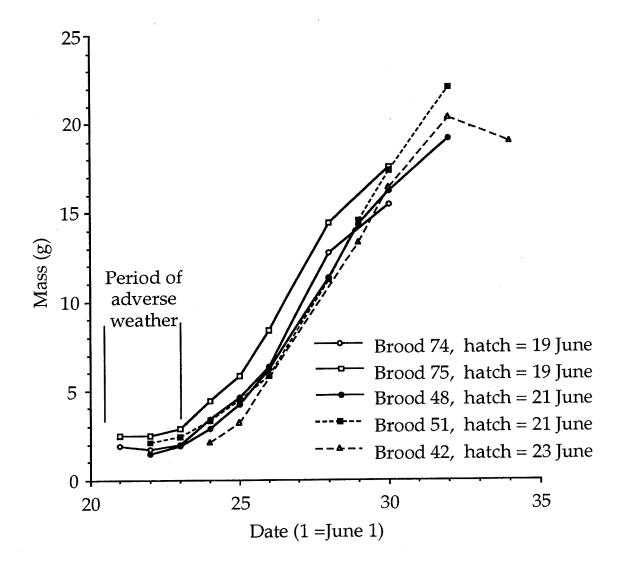


Figure 5.11. Growth of nestling tree swallows during and after a period of adverse environmental conditions. Broods 74 and 75 hatched at the begining of a four day period of cold, wet weather. Broods 48 and 51 hatched in the middle of this period, and brood 42 hatched when conditions had improved. Growth of brood 42 follows a normal growth trajectory similar to that shown in Figure 5.1.

that fledged from the three nests that hatched in the week immediately following the adverse weather (Table 5.6), suggesting that post-fledging survival was impaired.

DISCUSSION

The growth curve of the tree swallow is typical of small passerines. Several authors have noted that among Hirundinidae, as well as other aerial insectivores and some sea-birds, nestling mass exceeds adult mass and weight recession occurs before fledging (Edson 1930, Ricklefs 1968b). The tree swallow exhibits a small degree of weight recession before fledging, with the excess mass being due to the high water content of tissue (Figure 5.4a), as in other aerial insectivores (Ricklefs 1968b, O'Connor 1984). When examining the curves of individual tree swallows, it is evident that there is much fluctuation in mass between day 12 and fledging, rather than a steady decline, indicating that although the overall decrease may be associated with loss of water, nestling mass fluctuates on a shorter time scale. Although nestlings attained adult mass by day 10, the higher water content of these nestlings and its subsequent loss hides the fact that they continue to accumulate dry matter for most of the nestling period (Figure 5.3b).

Both of the bone structures measured, tarsus and manus, reached adult length by day 10. Rapid development of tarsus has been described as a possible adaptation for intra-brood competition during begging (O'Connor 1984), and rapid lengthening of the wing bones may be necessary to provide time for sufficient calcification before fledging (Carrier and Leon 1990, Carrier and Auriemma 1992). This rapid development of

Table 5.6. Fates of nestlings from broods hatching before and after the adverse weather of 19 - 23 June 1992. Number fledged and returned are those nestlings that were subsequently recaptured at the study site in 1993, while those fledged but not returned were not recaptured.

Nest	Hatch Date	Number Fledged and Not Returned	Number Fledged and Returned
74	19 June	5	0
7 5	19 June	4	0
48	21 June	5	0
51	21 June	2	1
42	23 June	6	0
82	24 June	3	2
55	28 June	1	3
206	28 June	5	1

bone structure is in contrast to the relatively slow growth of flight feathers. The ninth primary feather reaches only 60 - 70 % of its mature length prior to fledging, and a ninth primary of full adult length may not be attained until the first or even second prebasic molt (Robertson et al. 1992), a pattern seen in many passerines (Pyle et al. 1987). This is a surprising result for a species so dependent on flight for obtaining food and where selection on flight efficiency would be expected to be strong. However, Alatalo et al. (1984) have speculated that shorter outer primaries in young birds modify wing shape in such a way as to provide increased maneuverability at the expense of flight speed.

Variability in Tree Swallow Growth Rates

Growth of nestling tree swallows varied with breeding location, year, and hatch date. The variation in growth between the two Ithaca study sites, and among years at those sites (Table 5.2), suggests that most of the variability in growth seen among the previously published studies is due to micro-habitat differences and year effects, rather than an effect of the different regions of North America where these studies were conducted. Given the range of variation in both habitat and geographic region where these data were collected, the lack of greater variability relative to the Ithaca sites is somewhat surprising. All of the sites included lie in the middle of the species range: it would be informative to obtain growth data from more southerly nesting sites such as California and Georgia, as well as from the northern limits of breeding in Alaska, Yukon, and northern Quebec. The basis for the differences between the two Ithaca sites probably lies in the differences in the density of breeding birds, resulting in interference among

foragers, rather than differences in insect productivity (Chapter Three, Appendix One). A similar pattern of decreased nestling nutrition with increasing density of breeding pairs has been observed in fieldfares (*Turdus pilaris*; Wiklund and Andersson 1994). Differences among years are probably not related to nest density but to weather during nestling rearing. The lowest growth rate occurred in 1991, a year when most nestlings died during a period of poor weather in mid-June.

The general increase in growth rates with date within season is counter to the general trend in birds of decreasing reproductive success later in the season (e.g. von Haartman 1966, Stutchbury and Robertson 1988, Perrins and McCleery 1989, Hochachka 1990, Verhulst and Tinbergen 1991, Wiggins et al. 1994, D. W. Winkler and P. Allen unpublished data). Although the increase is small, it may be the result of a slight increase in both the abundance of food and its reliability that occurs in the latter part of the nesting season (Chapters Two and Seven).

These results support the results of previous studies suggesting the importance of micro-habitat differences in determining nestling growth in tree swallows (Quinney et al. 1986, Blancher and McNicol 1988, St. Louis and Barlow 1993) and suggest that the effects of weather are also highly significant, especially when comparing sites in different years (see Chapter Seven).

Comparison to other species of Hirundinidae

Given the similarity in ecology among species of swallows, it is interesting to note the degree of variability seen in growth rates among the Hirundinidae. Although it has been suggested that species that do not

attempt to rear more than one brood per season should have lower growth rates than double brooded species (Ricklefs 1984), the data for swallows do not support this hypothesis: single brooded species such as tree swallows have growth rates similar to those of facultatively double brooded barn swallows and bank swallows (Table 5.4). Swallows also seem to contradict the general pattern of slow growth in tropical species (Ricklefs 1968a). Of the three tropically breeding species (*Progne chalybea*, *P. tapera*, and *Hirundo tahitica*) only *P. tapera* shows an unusually low growth rate.

As a group the Hirundinidae has lower growth rates and longer nestling periods than other passerines of similar size (McCarty unpubl.). This pattern could be related to several aspects of the ecology of swallows, including their relatively large brood sizes, susceptibility to short-term fluctuation in food supply, relatively safe nest sites, or the necessity of greater development before fledging. If swallows do have safer nest sites, their slow growth would tend to support the trade-off between growth and mortality proposed by Lack (1968), who suggested that predation risk selected for faster growth, while starvation risk selected for slower growth. However, within the swallows there does not appear to be a correspondence between less exposed nest sites (e.g. T. bicolor, T. thalassina, H. pyrrhonota) and slower growth. The effects of the susceptibility of swallows to food shortages are difficult to predict. Although slower growth may decrease maximum energy demands (Lack 1968, Case 1978), rapid growth would limit the duration of the vulnerable period (Lack 1968, Winkler 1993). Rapid growth would also be predicted if larger brood members had a higher probability of surviving food shortages (O'Connor 1977b). Although adult body mass and brood size together can

account for some of the difference in growth between swallows and other passerines (Ricklefs 1968), there remains a tendency for swallows to show slower development that remains to be explained, possibly by integrating other aspects of the ecology of these groups, such as foraging mode (McCarty unpubl.).

Post-Fledging Survival

The pattern of reduced post-fledging survival in nestling tree swallows with below average growth or fledging size is typical of other species of passerines (Perrins 1965, 1988; Garnett 1981; Nur 1984; Davies 1986; McGowan 1987; Gustafsson and Sutherland 1988; Tinbergen and Boerlijst 1990; Gebhardt-Heinrich and van Noordwijk 1991; Magrath 1991; Lindén et al. 1992, but see Ross and McLearn 1981, Nur and Clobert 1988, Sullivan 1989). This result is in contrast with the result of DeSteven (1980) who found no relationship between nestling size and post-fledging survival in her study of tree swallows. This difference could be due the relatively small sample size (417 fledglings) and short duration (one year) of DeSteven's study. The present study drew on a larger sample of fledglings (> 1500) and includes information from more years. Although the trend for each year was the same, I did find that the magnitude of the effect of nestling size on survival differed among years (McCarty unpubl.).

The relationship between nestling growth and survival appears to be a causal one; experimental manipulations of nestling growth in great tits (*Parus major*) suggest that reduced growth *per se*, rather than a correlated factor such as parental quality or environmental conditions is resulting in lower postfledging survival (Tinbergen and Boerlijst 1990).

This result is also supported by the differential survival of nestlings with different growth rates from the same brood (Tinbergen and Boerlijst 1990). Although a reduction in overall return rate with experimentally reduced growth was not found in this study, a relationship was found between the amount of mass lost and the probability of return among the experimental broods. The lack of a difference in return rates between the experimental broods and the controls is not surprising given that sample sizes were small.

The mechanism behind the relationship between nestling growth and post-fledging survival remains unclear. Perrins (1965) attributed the relation between nestling size and survival in great tits to the higher energy reserves available to the heavier young birds, which is supported by differences in body composition found in fledgling blue tits (O'Connor 1976). This interpretation has been challenged by Garnett (1981) who calculated that differences in fat reserves are probably not able to significantly influence survival. Garnett presented evidence for an alternative interpretation based on indirect effects of body size acting through dominance and social interactions. Reduced growth may have a long-term effect on fitness, even when it does not appear to result in lower post-fledging survival, by decreasing the ability to obtain a breeding territory or mate or by lowering subsequent fecundity. Slow growth in nestling carrion crows results in smaller adults who are subordinate and less likely to become breeders (Richner 1989, 1992; Richner et al. 1989, see also Gustafsson and Sutherland 1988). A similar effect of size may occur in tree swallows, where larger, heavier males are more likely to successfully defend nest-boxes (Lozano 1994). The lack of a relationship between body

size and fat stores in tree swallows suggests that increased energy stores are not responsible for the differences in survival, but rather that some other effect of growth rate or body size is the mechanism responsible for increased fledgling survival in faster growing nestlings (Chapter Six).

Changes in Body Composition

The growth of body components in nestling tree swallows follow two general trends; 1) decreasing water content with age, and 2) a shift in emphasis from tissues devoted to growth to tissues required for independence. A decrease in the percent water in tissue (or water index) is universally observed in the development of nestling passerines, and has been suggested as an indication of the maturity of tissue (Ricklefs 1979, Ricklefs and Webb 1985, but see Marsh and Wickler 1982). Water content seems to correlate with functional measures of maturity, such as thermoregulatory ability (Ricklefs and Webb 1985), and correlate well with overall growth and development in a variety of species (Konarzewski 1988). The internal organs have the lowest water content and reach the adult level of water content before the other major body components, indicating that these tissues are the first to mature. Among the internal organs examined, this trend is most evident in the gastro-intestinal tract and liver, while the other organs, including the heart, mature more slowly.

The allocation of biomass to different tissues, as measured by percent of total dry mass, shows a shift with age from an emphasis on tissues related to further production (e.g. liver and gastrointestinal tract) to an emphasis on tissues necessary for post-fledging survival (e.g. feathers and

pectoralis muscles). The use of dry mass as a measure of biomass and energy allocation assumes that different tissues have similar compositions, however, little information is available to evaluate the validity of this assumption for passerines. Patterns of growth of various body components tend to be similar to those of other passerines (O'Connor 1977a, Lilja 1983, Tatner 1984, Clum 1991), with liver and intestines being relatively large early in development, pectoralis muscles and feathers increasing later in development, and little change observed in the relative size of the heart and other internal organs such as lungs. These patterns are found in species that differ widely in life history and ecology, such as the magpie (*Pica pica*; Tatner 1984), boat-tailed grackle (*Quiscalus major*; Clum 1991), blue tit and house sparrow (*Parus caeruleus* and *Passer domesticus*; O'Connor 1977a). Not surprisingly the pattern found in the tree swallow most closely resembles that observed in the house martin (*Delichon urbica*; O'Connor 1977a).

It appears that both the patterns of tissue maturity and relative allocation of biomass support the predicted pattern of early emphasis on organs devoted to future production with later development of organs devoted to locomotion and thermoregulation (e.g. pectoralis muscles).

Effects of Short-Term Reductions in Growth

The results of the fasting experiment indicate that short-term reductions in growth have long-term effects on the subsequent growth and size of nestling tree swallows (Table 5.5). Given the relationship between growth and post-fledging survival in this population (Table 5.1), these effects on growth may in turn translate into significant effects on fitness.

Although the small sample sizes in this experiment were not sufficient to detect a difference in post-fledging survival between the starved and control groups, the relationship between mass lost and probability of return within the starved group suggests that short-term reductions in growth will influence survival. This conclusion is further supported by the results of the natural growth reductions observed in 1991, which also reduced post-fledging survival.

The conclusions of this study differ from those of Wiggins (1990), who found no long-term effects of reduced nestling growth in tree swallows. There are several possible explanations for the differences in results. Wiggins produced differences in growth by removing one or two nestlings from each brood for periods of four hours on four consecutive days and then compared the growth of these "deprived" nestlings to their siblings who had not been removed. This type of manipulation provides more opportunity for parents to compensate for the reduced state of the "deprived" nestlings since they feed a reduced brood during the period of the experiment. The manipulation performed in this study more closely matches the conditions experienced by both nestlings and parents during periods of poor environmental conditions; the entire brood experiences a food shortage for an extended period and the parents must then contend with an entire brood of deprived nestlings when conditions return to normal. Conditions in nature under which only a portion of a brood are deprived, as in Wiggins experiment, are more difficult to envision. A second problem lies in Wiggins' interpretation of his results. The "deprived" nestlings in his experiment were significantly heavier than their siblings prior to manipulation, and they were both smaller and

lighter than their siblings at the end of the experiment. However, this initial difference in mass was not accounted for in the statistical tests, resulting in an overly conservative test and an increased risk of a type II error.

The ability to temporarily interrupt growth and development during periods of poor weather has been cited as a possible adaptation to short-term fluctuations in food supply (O'Connor 1977b, Emlen et al. 1991). Although nestling tree swallows certainly exhibit an interruption in both growth and development, the results of the growth experiment and natural interruptions in growth show that this is not without a cost. Only investigations of this phenomenon in other species that are not naturally subject to short-term food shortages could discriminate between the two possibilities: that the ability to interrupt growth is a special adaptation of aerial insectivores for surviving periods of low food availability, or that interruption in growth is an unavoidable byproduct of low body temperatures and low food intake in "normal" passerines. Although aerial insectivores are able to survive long periods at low body temperatures (e.g. Prinzinger and Siedle 1986, 1988), low body temperatures have been documented in a variety of passerine species (e.g. Dawson and Evans 1957, Olson 1992), as have reduced growth and interrupted development during periods of low food abundance (e.g. Dickerson and McCance 1960, McCance 1960, Ricklefs and Peters 1979, Price 1985). Given the long nestling period and potential for temporary reductions in food supply, it is not surprising that interrupted growth is most often observed in aerial insectivores; it remains to be tested whether low body

temperatures and interrupted growth in aerial insectivores are special adaptations to an unpredictable food supply.

Conclusions

The pattern of growth in nestling tree swallows is typical of other passerines, showing a rapid growth in both mass and structural size. Of the major body components, only feather development is not complete prior to fledging. Tissues continue to lose water throughout the nestling period, indicating that tissue development and accumulation of dry mass continues long after peak mass is reached. Both tissue maturity and allocation of biomass follow the pattern observed in other passerines of early emphasis on organs related to production (such as the gastro-intestinal tract) and much later emphasis on organs (such as pectoralis muscles and feathers) that are necessary for post-fledging survival. Growth of nestling tree swallows is highly variable and influenced by a variety of environmental factors, including weather conditions, nesting habitat and location, year, and season. Reductions in growth are related to reduced post-fledging survival, and even short-term interruptions in growth may have profound long-term effects.

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CHAPTER SIX:

Changes in Energy Reserves and Fasting Capacity with Age in Nestling Tree Swallows

INTRODUCTION

Short-term changes in environmental conditions are an important source of mortality and reproductive failure in birds (Lack 1954, Smith and Webster 1955, Boyd 1957, Dobinson and Richards 1964, Ogilvie and St. Joseph 1976, Marcström and Mascher 1979, Reynolds 1979, Marti and Wagner 1985, Elkins 1988). Aerial insectivores such as swallows, swifts, and bee-eaters are especially susceptible to fluctuations in environmental conditions which result in mortality of both adults and nestlings (Edson 1943, Koskimies 1950, Lack and Lack 1951, Gladwin and Nau 1964, Elkins and Etheridge 1974, Wrege and Emlen 1991, Hill and Chambers 1992). Tree swallows (*Tachycineta bicolor*) are the earliest breeding of the North American swallows (Bent 1942, Sheppard 1977) and are especially susceptible to these fluctuations, which cause mortality among both adults and nestlings (Dence 1946, Weatherhead et al. 1985, Lombardo 1986, Littrell 1992).

Unpredictable, short-term variation in environmental conditions such as those experienced by tree swallows, make avoidance of adverse conditions impossible. Populations subject to mortality due to unpredictable changes in conditions would be expected to evolve strategies that prolong the length of time individuals can survive such conditions. This chapter examines how energy reserves of nestling tree swallows change through development, and the effects of these changes on fasting capacity.

Adverse conditions for nestling tree swallows include combinations of low ambient temperatures and low food availability. Several strategies are available to tree swallows under such conditions; energy intake can be increased, energy reserves can be increased, or energy demands can be decreased. Given the constraints on swallow foraging (Chapters Two and Three) the ability of adult swallows to increase food delivery is probably limited. Nestlings do have the potential to either increase reserves or temporarily decrease demands. I compare the energy reserves and body compositions of normal nestlings to nestlings that died during periods of cool rainy weather and calculate predicted fasting endurance under different ambient temperatures. Finally, I address the possibility that tree swallows are sequestering unusually large levels of fat as insurance against periods of low food availability by comparing the fat stores of aerial insectivores to other species that raise their nestlings on a diet of insects.

Nestling energy demands can also be decreased by lowering the use of energy in maintenance or production. Since both maintenance and production costs are strongly influenced by body temperature, the use of torpor might be an adaptation to decrease mortality associated with brief periods of adverse environmental conditions. Tree swallow nestlings frequently exhibit low body temperatures during periods of unfavorable environmental conditions, and low body temperatures are associated with low metabolic requirements (Chapter Three). Nestlings and adults of other swallow species are known to be capable of using torpor to increase their ability to survive periods of low food (Lasiewski 1966; Serventy 1970; Prinzinger and Siedle 1986, 1988). I present the results of an experiment on the effect of ambient temperature on mass loss during fasting which

corroborate the utility of torpor in decreasing the rate of mass loss in nestlings. I also present data on the range in nestling body temperatures under naturally occurring periods of adverse weather to determine if tree swallows are using such a strategy to increase nestling survival.

METHODS

Tree swallows breeding in nest-boxes were studied at the Cornell University Experimental Ponds Facility (42° 30' N; 76° 27' W), near Ithaca, New York. This facility consists of two breeding sites, Unit One with approximately 55 - 75 pairs of tree swallows, and Unit Two with between 10 and 23 pairs. Swallows breeding at these sites are monitored closely to determine the date of hatching and nestling age. Nestlings were weighed to the nearest 0.1 g during the 1990 - 1993 breeding seasons using either a Pesola spring scale or a portable electronic balance. Lengths of the flattened, straightened wing, ninth primary, first secondary, and sixth rectrix were measured to the nearest 0.5 mm using a ruler with a wing or feather stop. Tarsus length was measured to the nearest 0.1 mm using dial calipers.

Body composition and fat reserves

Nestlings that died during periods of cold rainy weather were collected in June 1992 (referred to subsequently as dead nestlings). A small number of nestlings that died during similar conditions in 1988 and 1990 were also included in determination of body fat but not in calculations that included body water content. Only one nestling from each brood was

included. All nestlings came from known-age nests and were collected, placed in plastic bags, and frozen within 24 to 48 hours after death. Some breakdown of fats may have occurred between death and collection of these nestlings; however, ambient temperatures were generally well below 15°C, and badly decomposed individuals were not used in these analyses. It is assumed in these analyses that loss of fat after death in these nestlings was negligible.

During June 1993, a sample of nestlings (referred to subsequently as healthy nestlings) of known age were killed using CO2 inhalation. Nestlings were immediately weighed to the nearest 0.1 g using a portable electronic balance, placed in plastic bags, and frozen until analysis. Healthy nestlings were collected on nestling days 3, 6, 9, 12, and 15, where hatch day = day 1. At each age, all healthy nestlings were taken from different broods; additional nestlings were taken from these broods at subsequent ages. Several fledglings of unknown age were collected in July 1992. Although these fledglings were not hatched from the main study colony, they are estimated to be between 30 and 50 days of age based on fledging dates of other nests in the area. Adults found dead near the study area were salvaged and assigned to either healthy or starved categories depending on the cause of death. Those adults killed by cars, predators, or nest-box competitors were considered healthy at the time of death while those found dead in nest-boxes during inclement or cold weather were considered to have starved to death.

At the time of analysis, birds were re-weighed and morphological measurements taken. All feathers were removed, the carcass dissected, and stomach contents removed. Pectoralis muscles, gastrointestinal tract, liver, and heart were weighed separately on an analytical balance. The remaining internal organs (lungs, kidneys, and gonads) were removed and weighed as a group. Finally, the remaining body components (head, bones, and remaining muscles) were weighed. All tissues were dried at 60 - 70 °C until three consecutive weighings showed no further decrease in mass (Kerr et al. 1982, Williams and Prints 1986, Taylor and Konarzewski 1989); water content was calculated from the mass loss during drying. Water Index, defined as:

Water Index =
$$\frac{\text{grams of water}}{\text{lean dry mass}}$$
 (6-1)

was calculated for the pooled body components of each nestling.

Dried tissue was ground in an electric food processor and extracted in Soxhlet extractors using chloroform solvent. Fat content was calculated from mass loss during extraction. To obtain a sufficient sample for fat extractions, all body components from an individual were pooled for fat extractions. For larger nestlings and adults, dried tissue was divided into two samples for extraction. Since the two samples represent the total tissue of an individual, results from the two samples were combined for analysis. Fat Index, defined as:

$$Fat Index = \frac{grams of fat}{lean dry mass}$$
 (6-2)

was calculated for each individual.

Chloroform may extract structural lipids that are not available for energy metabolism, in addition to lipid available as energy stores (Dobush

et al 1985, Blem 1990). I corrected for the extraction of unavailable structural lipids in the determinations of energy reserves and fasting capacity by subtracting the amount of fat remaining in dead nestlings of a given age from the fat extracted from healthy nestlings of the same age (Blem 1990), based on the assumption that nestlings under similar environmental conditions die at similar fat contents (Zimmerman 1965, Pope and Ward 1972). The use of ether solvent is thought to avoid the problem of extracting structural fats (Blem 1990), but this correction must still be applied since individuals may have some fat stores remaining after death. Using chloroform to measure total fat has the advantage of removing a larger percentage of lipids, thus providing a better estimate of the protein content of fat-extracted tissue for use in estimating the energetics of growth and energy reserves (Dobush et al. 1985).

Means of body components were compared using Mann-Whitney U-tests. Sample sizes for different body components varied; see Appendix Two. For comparisons between body compositions of healthy and dead nestlings, dead nestlings were assigned to age categories based on their age at time of death. Since growth and development is slowed during periods of fasting (Chapter Five), these nestlings were assigned to age categories equal to or lower than their actual age. Nestlings that died on days 4 or 5 were assigned to the day 3 category, those that died on days 7 and 8 were placed in the day 6 category, and those that died on days 10 and 11 were assigned to the day 9 category. The day 12 category includes only nestlings that died on days 14, 15 and 16. Finally, the fledged category includes nestlings that died on days 20 - 30, even if the nestlings had not left their nest. This

categorical analysis was chosen over one based on regression techniques using nestling age as a continuous variable because of the small sample sizes in some age groups and unequal distributions of ages between the two groups. Such groupings are conservative in that they control for some of the retarded growth and development that nestlings show prior to death (Chapter Five).

Estimates of Fasting Capacity

The relevance of energetic stores to the ability of birds to survive can be estimated by comparing the amounts of fat and protein available to an estimate of the rate of energy use. Typically, this involves comparing the fat and protein content of the individuals of interest to fat and protein remaining in individuals that have died under conditions of interest (e.g. Jenni and Jenni-Eiermann 1987, Piersma 1988, Thompson and Flux 1988, Taylor and Konarzewski 1989, Navarro 1992, Lovvorn 1994). This method does not necessarily assume that the depletion of energy stores are the mechanism of death, only that the remaining energy stores are correlated with the time of death.

Fasting capacity of tree swallows of different ages were estimated by calculating the fat and protein reserves of healthy birds and dividing by the appropriate resting metabolic rate (RMR; Chapter Four). Fat content of nestlings that had died during periods of inclement weather (i.e. dead nestlings) averaged 2.2 percent of their total wet mass over all ages (see Results). Available fat reserves of healthy nestlings were thus calculated as their total fat minus 0.022 times their total wet mass. This value was then converted to kJ of reserves based on a conversion of 39 kJ g⁻¹ fat (Ricklefs

1974). The relationship between pectoralis dry mass and wing length in dead nestlings was used to estimate the available dry mass of pectoralis for healthy nestlings. The relationship between pectoralis dry mass and wing length in dead nestlings is:

dry mass of pectoralis =
$$0.004 * (wing length) - 0.03$$
 (6-3)

with $R^2 = 0.892$ and p = 0.0001. This equation was used to estimate the dry mass of pectoralis that would remain if a healthy nestling of a given wing length were to die during inclement weather conditions. This estimate was then subtracted from the healthy nestling's pectoralis mass to estimate the amount of muscle available as an energy reserve. This muscle mass was assumed to be 90 % protein, and reserves were calculated using a value of 18 kJ g⁻¹ muscle (Ricklefs 1974). Since nitrogen content of dry pectoralis muscles in other passerines stays relatively constant as nestlings grow and mature (Clum 1991), no age adjustment was included in the determination of content. Total energy reserves were then divided by the appropriate resting metabolic rate for nestlings of each age (see Chapter Four) and for adults (Williams 1988) to determine the fasting capacity in hours (Jenni and Jenni-Eiermann 1987, Thompson and Flux 1988, Taylor and Konarzewski 1989, Navarro 1992, Lovvorn 1994).

The Effects of Temperature on Mass Loss During Fasting

To determine the effects of temperature on mass loss during fasting, broods of nestlings were fasted on day 6. Day 6 was chosen because nestlings of this age are growing rapidly (Chapter Five) and have some

ability to thermoregulate if they are with brood-mates (Dunn 1979). Broods were randomly assigned to either cold (20°C) or hot treatments (30°C). Initial mass was measured in the morning when nestlings were removed from the nest (between 0630 and 0730 h). One or two nestlings from a nonexperimental nest were placed in each nest-box to keep the parents from abandoning the nest while their chicks were gone. Each brood was placed in a lined tree swallow nest built in a cardboard box (salvaged from previously abandoned nests). Nestlings were fasted in controlled temperature chambers at either 20°C or 30°C under a weak incandescent lamp to simulate nest-box lighting conditions. Chamber temperatures and nestling body temperatures were measured using type-T thermocouples. All body temperatures were measured by inserting a fine gauge thermocouple into the nestlings proventriculus. Final mass was measured between 1730 and 1845 h in the evening, and nestlings were returned to the nest immediately after this evening mass measurement. For statistical purposes, each brood was treated as an experimental unit and the mean masses for the chicks within a nest were compared.

Body Temperatures of Wild Nestlings

The body temperatures of wild nestlings were measured using typeT thermocouples inserted into the nestlings' proventriculus.

Measurements were collected opportunistically during 1992 and 1993 on a set of days chosen to represent a range of environmental temperatures.

Nests were approached in a car, the entire nest (in a cardboard nest-liner) quickly removed, and a thermocouple inserted into one nestling within 60 s of approaching the nest (Dunn 1979). This "grab and jab" method, rather

than remote monitoring of nestlings with implanted thermocouples, was used because the intent of the measurements was to provide a survey of the effects of ambient temperature on the body temperatures of a large sample of nests. It was not intended to give a measure of the absolute body temperature of individual nestling tree swallows.

RESULTS

Environmentally related mortality of nestling tree swallows can have profound effects on the reproductive success of tree swallows. Although mortality in many years is as low as 15 - 20 %, in some years it climbs as high as 50 - 60 % (Figure 6.1a). Mortality of this magnitude even has implications for the size of the breeding population; the change in the number of breeding pairs at the main study site is significantly correlated with the number of chicks fledged in the previous year (Figure 6.1b).

Body composition and fat reserves

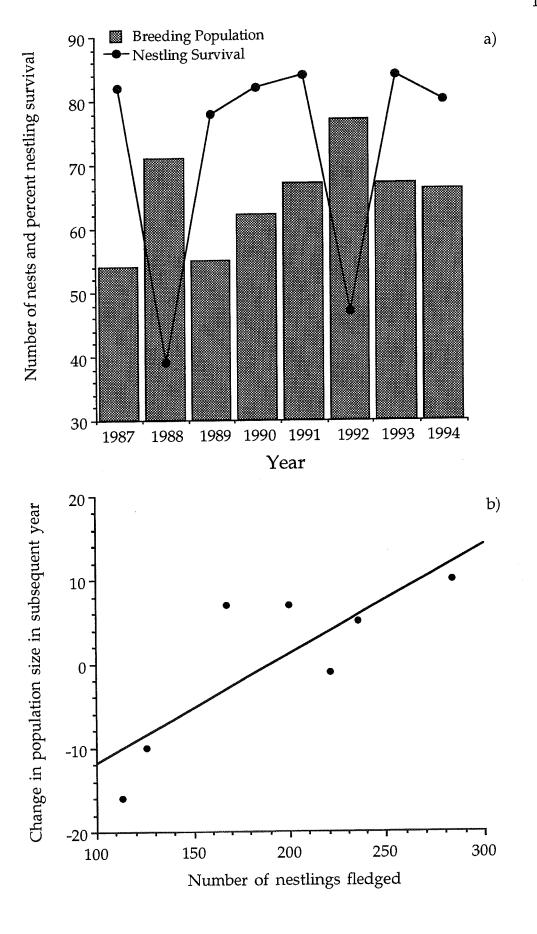
Fat reserves of nestlings increased with age. Total grams of fat, grams of fat divided by wet mass, and fat index all show significant increases with age (Figures 6.2a-c). Lean dry mass shows a similar pattern of increase (Figure 6.2d). Among healthy nestlings, fat content, as measured by Fat Index, of day 12 and 15 nestlings was not correlated with body mass (day 12 r = 0.22, p = 0.64; day 15 r = 0.03, p = 0.95), tarsus length (day 12 r = -0.56, p = 0.25; day 15 r = 0.10, p = 0.81), wing length (day 12 r = 0.09, p = 0.86; day 15 r = -0.18, p = 0.67), or feather length (day 12 r = -0.16, p = 0.74; day 15 r = -0.20, p = 0.63). Sample sizes are small (7 for day 12 and 8 for day 15) so the probability of type-II error is high. However, it is interesting

to note that the correlations were as likely to be negative as they were to be positive, indicating that if a relationship does exist, it is weak.

Nestlings that died during periods of inclement weather ("dead nestlings") show a reduction in virtually every aspect of their growth when compared to healthy nestlings of similar ages. Tarsus length, flattened, straightened wing chord (hereafter, wing chord), and ninth primary length, as well as total mass all show some degree of retardation in nestlings that died during periods of inclement weather (Figure 6.3). The actual degree of retardation is actually greater than indicated by this analysis because of the age categories used (see Methods).

The dry masses of the internal organs taken as a whole of dead nestlings were significantly lower than those of healthy nestlings of the same age (Figure 6.4a). Dry masses of the gastrointestinal (GI) tract, liver, heart, and remaining organs were lower in dead nestlings than in healthy nestlings (Figures 6.4b-e); however, these differences in individual organs were significant for day 15 nestlings only. Organ masses of adults did not differ between the starved and healthy groups. Although organ masses for starved nestlings were smaller on an absolute scale, when looking at the dry mass of internal organs as a percent of the total body mass, the internal organs actually make up an equal or greater portion of the total body in dead nestlings compared to healthy nestlings (Figure 6.5a). The same pattern is seen in the individual organs (Figure 6.5b-e). When corrected by linear size (by dividing by wing length), however, the dry mass of organs are lower for starved nestlings pooled across all ages. The mean mass of internal organs divided by wing length is 0.025 g/mm (st. dev. = 0.006) for healthy nestlings and is 0.016 g/mm (st. dev. = 0.008) for dead nestlings

Figure 6.1. Relationship between fledging success and population size of tree swallows at Cornell Experimental Ponds Unit One. Data from 1987 - 1994. The number of nestlings fledged (line graph on Figure 6.1a) and number of breeding pairs at Unit One (bars on Figure 6.1a) are given for each year. Number of breeding pairs is defined as the number of nests that contained eggs before 1 June, in order to eliminate re-nesting attempts. There is a significant relationship between the number of fledglings produced at Unit One and the change in the number of breeding pairs present in the subsequent year (Figure 6.1b; $R^2 = 0.656$. p = 0.027).



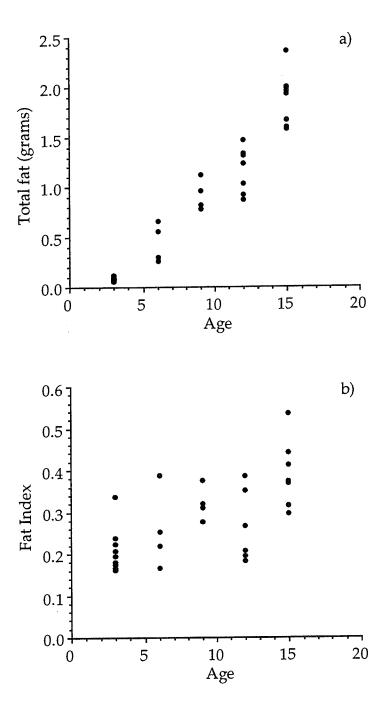
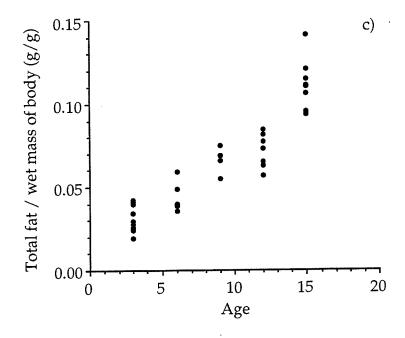
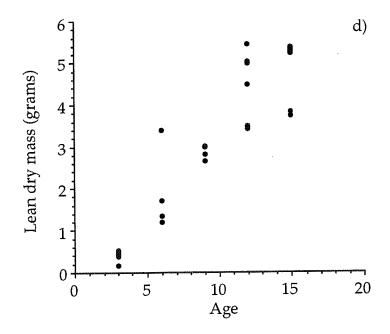


Figure 6.2. Fat content and lean dry mass of healthy nestling tree swallows of different ages. Least squares regression of total fat content on age of nestlings (Figure 6.2a) results in R2 = 0.926, p = 0.0001, n = 35. Least squares regression of Fat Index on age of nestlings (Figure 6.2b) results in R2 = 0.454, p = 0.0001, n = 35. Least squares regression of total fat content divided by total wet mass on age (Figure 6.2c) results in R2 = 0.859, p = 0.0001, n = 35. Least squares regression of total lean dry mass on age (Figure 6.2d) results in R2 = 0.91, p = 0.0001, n = 35.

Figure 6.2 (continued)





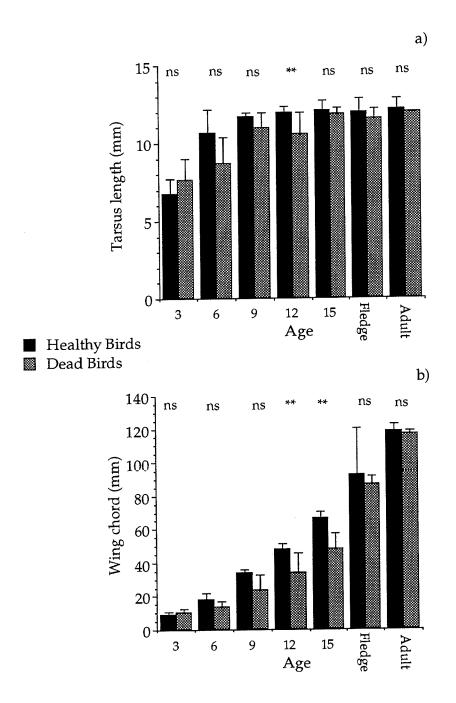
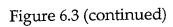
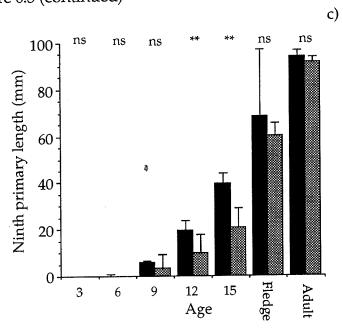
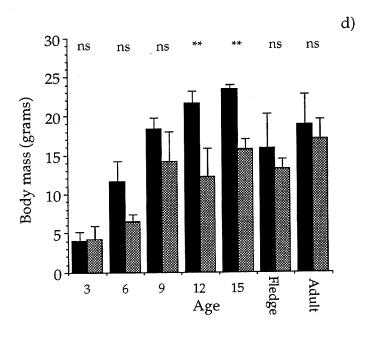


Figure 6.3. Tarsus length, wing length, and length of the ninth primary of normal (healthy) nestlings and those that died during periods of bad weather (dead nestlings). Healthy and dead nestlings were compared using Mann-Whitney U-tests. For each age category a sequential Bonferroni adjustment (Rice 1989) was applied across measurements shown in this figure. ns = Bonferroni-adjusted p \geq 0.10, * = 0.05 \leq Bonferroni-adjusted p < 0.10, ** = Bonferroni-adjusted p < 0.05. See Appendix Two for sample sizes.







Healthy Birds Dead Birds

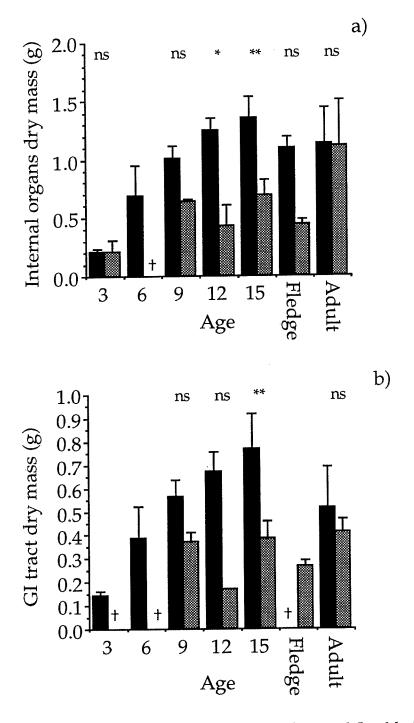
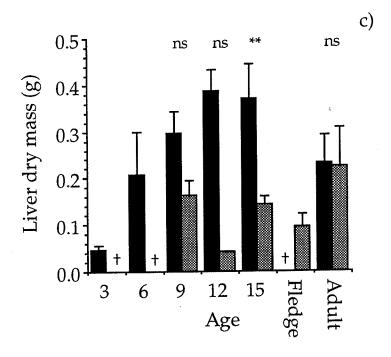


Figure 6.4. Dry mass of the internal organs of normal (healthy) nestlings and those that died during periods of bad weather (dead nestlings). Other internal organs consist primarily of lungs, kidneys, and gonads. Healthy and dead nestling were compared using Mann-Whitney U-tests. For each age category a sequential Bonferroni adjustment (Rice 1989) was applied across measurements shown in this figure. ns = Bonferroni-adjusted p \geq 0.10, * = 0.05 \leq Bonferroni-adjusted p < 0.10, ** = Bonferroni-adjusted p < 0.05. See Appendix Two for sample sizes.

Figure 6.4 (continued)



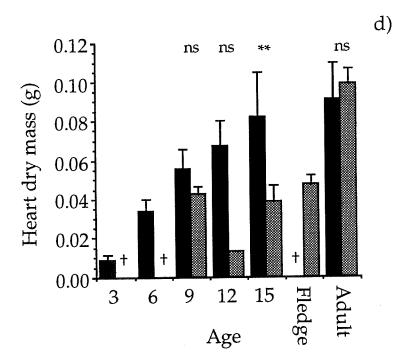
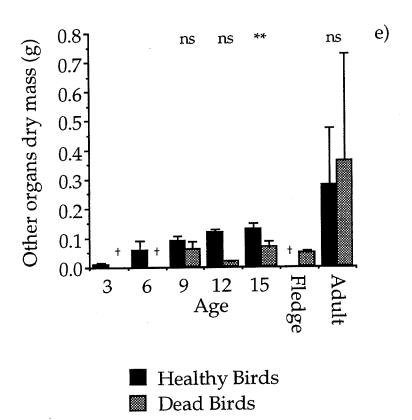


Figure 6.4 (continued)



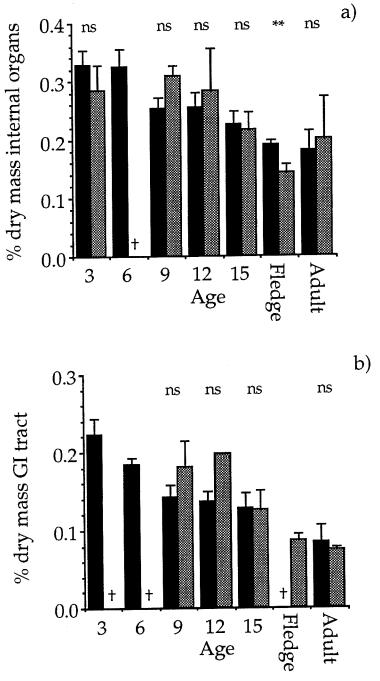
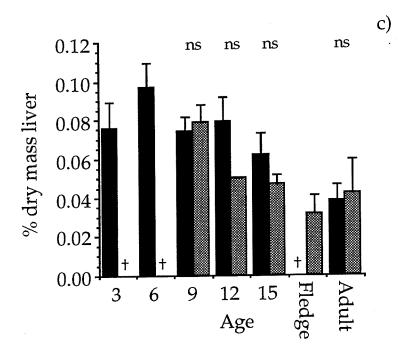


Figure 6.5. Percent of total body dry mass of the internal organs of normal (healthy) nestlings and those that died during periods of bad weather (dead nestlings). Other internal organs consist primarily of lungs, kidneys, and gonads. Healthy and dead nestling were compared using Mann-Whitney U-tests. For each age category a sequential Bonferroni adjustment (Rice 1989) was applied across measurements shown in this figure. ns = Bonferroni-adjusted $p \ge 0.10$, * = 0.05 \le Bonferroni-adjusted p < 0.10, ** = Bonferroni-adjusted p < 0.05. † = no data available. See Appendix Two for sample sizes.

Figure 6.5 (continued)



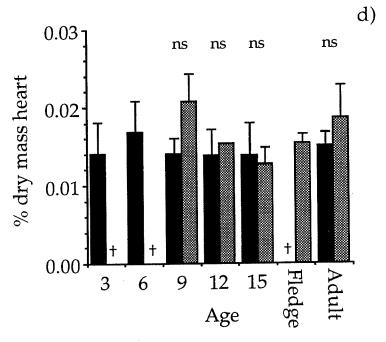
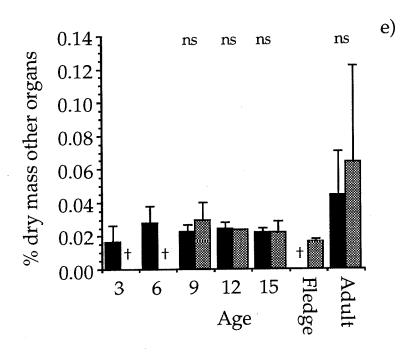


Figure 6.5 (continued)



- Healthy Birds
- Dead Birds

(Mann-Whitney U-test, p = 0.0002). The reduction in the absolute mass of internal organs and in organ mass corrected for linear size indicates that growth of these organs is retarded, while the tresult that the internal organs actually make up a larger percentage of total body mass in dead nestlings indicates that these organs are less retarded than the other body components.

In contrast, the pectoralis muscles show a significant reduction in dead nestlings both in terms of total dry mass (Figure 6.6a) and percent of total dry mass (Figure 6.6b). Pectoralis mass relative to wing length is not significantly reduced in dead nestlings. The mean mass of pectoralis muscle divided by wing length for all nestlings pooled is 0.004 g/mm (st. dev. = 0.003) for healthy nestlings and is 0.003 g/mm (st. dev. = 0.001) for dead nestlings (Mann-Whitney U-test, p = 0.15). The remaining body components (head, bones, and remaining muscles) follow a pattern similar to the internal organs, with dry mass being greater in healthy nestlings (Figure 6.6c) but with the percent of the total body mass being greater in dead nestlings (Figure 6.6d).

The water balance of dead nestlings does not appear to have been adversely affected by inclement weather. Both the percent of the total mass made up of water (Figure 6.7a) and the water index (Figure 6.7b) are higher in dead nestlings compared to healthy nestlings.

Fat reserves of dead nestlings were significantly reduced, compared to healthy nestlings of the same age (Figure 6.8a). These differences remain when correcting fat reserves for body size using either grams fat divided by wet mass (Figure 6.8b) or fat index (Figure 6.8c). With the exception of adults, the fat stores per gram of body mass remaining in dead birds is

consistent across ages. Fat reserves of all nestlings pooled are also reduced in dead nestlings, when total fat is adjusted for structural size (by dividing by wing length). Healthy nestlings had a mean of 0.020 g fat / mm (st. dev. = 0.009), while dead nestlings contained 0.007 gm fat / mm (st. dev. = 0.004; Mann-Whitney U-test, p < 0.001). Dead nestlings also show a significant reduction in fat free biomass, when corrected for structural size using wing length. Healthy nestlings had 0.072 gm fat-free dry mass / mm wing length (st. dev. = 0.024), while dead nestlings had 0.057 gm fat-free dry mass / mm wing length (st. dev. = 0.024).

Fasting Capacity

Available energy reserves increase steadily through development, reaching a peak in day 15 nestlings, and decreasing slightly in fledglings and adults (Table 6.1). A similar pattern is seen in the estimated fasting capacity of nestlings, which is generally highest in day 15 nestlings. Nestlings in this category are predicted to be capable of surviving 34 to 43 hours without food (Table 6.1). The exception to this pattern is day 3 nestlings, whose fasting capacity at 20°C is predicted to be over 40 hours. The predicted fasting endurance is predicted to be 3 - 30 hours longer at 20°C in nestlings which do not expend energy thermoregulating (Chapter Four), and 8 - 12 hours longer at 30°C for those that do thermoregulate.

The Effects of Temperature on Mass Loss During Fasting

Mean nestling body temperatures for the 30°C treatment was 36.3°C (n=10, STD = 2.0), and 21.5°C (n = 10, STD = 1.7) for the 20°C treatment. Chamber temperatures remained within 2°C of the prescribed

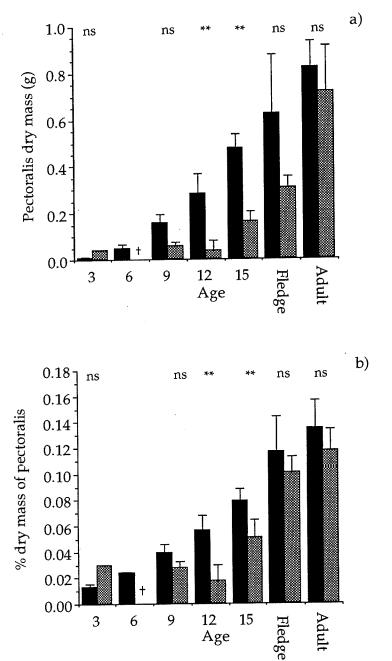
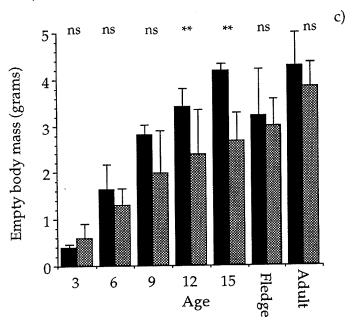
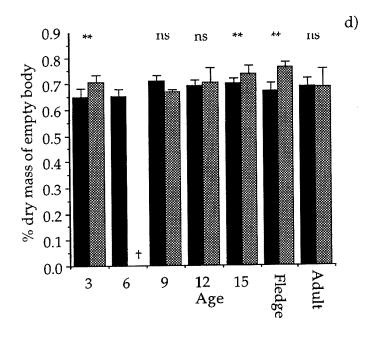


Figure 6.6. Dry mass and the percent of total body dry mass of the pectoralis muscles and the remaining body components (head, bones, and remaining muscle) of normal (healthy) nestlings and those that died during periods of bad weather (dead nestlings). Healthy and dead nestling were compared using Mann-Whitney U-tests. For each age category a sequential Bonferroni adjustment (Rice 1989) was applied across measurements in Figures 6.6a and 6.6c and across measurements in Figures 6.6b and 6.6d. ns = Bonferroni-adjusted p ≥ 0.10 , * = 0.05 \leq Bonferroni-adjusted p < 0.10, ** = Bonferroni-adjusted p < 0.05. † = no data avaiable. See Appendix Two for sample sizes.

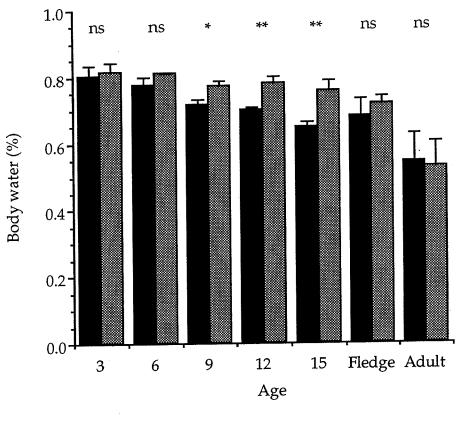
Figure 6.6 (continued)

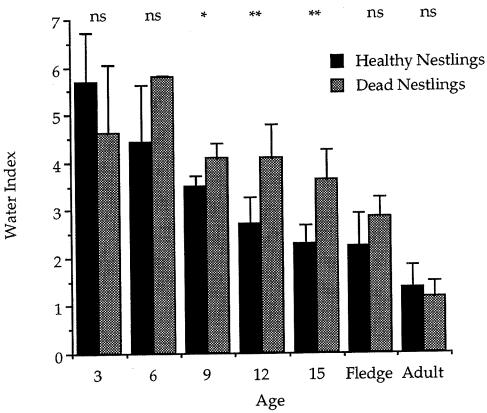




Healthy Birds
Dead Birds

Figure 6.7. Percent body water and Water Index in normal (healthy) nestlings and those that died during periods of bad weather. Healthy and dead nestling were compared using Mann-Whitney U-tests. For each age category a sequential Bonferroni adjustment (Rice 1989) was applied across measurements shown in this figure. ns = Bonferroni-adjusted p \geq 0.10, * = 0.05 \leq Bonferroni-adjusted p < 0.10, ** = Bonferroni-adjusted p < 0.05. See Appendix Two for sample sizes.





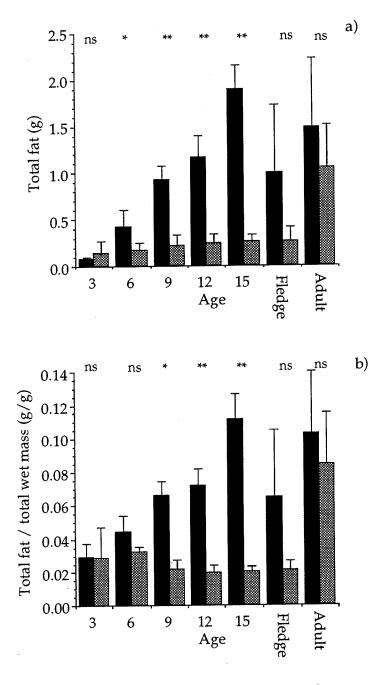
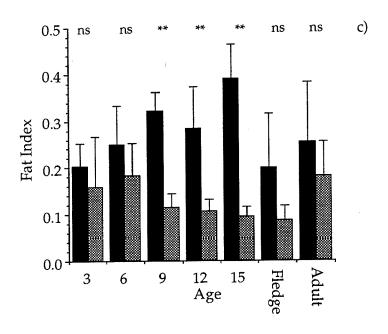


Figure 6.8. Grams of fat, fat reserves, and Fat Index corrected for wet body mass in normal (healthy) nestlings and those that died during periods of bad weather (dead nestlings). Healthy and dead nestling were compared using Mann-Whitney U-tests. For each age category a sequential Bonferroni adjustment (Rice 1989) was applied across measurements shown in this figure. ns = Bonferroni-adjusted p \geq 0.10, * = 0.05 \leq Bonferroni-adjusted p < 0.10, ** = Bonferroni-adjusted p < 0.05. See Appendix Two for sample sizes.

Figure 6.8 (continued)



Healthy Nestlings Dead Nestlings

temperatures; mean temperatures were 29.7°C (n = 7, STD = 0.8) for the 30°C or "hot" treatment and 18.7°C (n = 7, STD = 1.7) for the 20°C or "cold" treatment.

Mass losses of nestlings in the hot treatment were greater than those in the cold treatment over the twelve hours of the experiment. Broods in the hot treatment lost an average of 1.1 grams per nestling, while broods in the cold treatment lost an average of 0.2 grams per nestling (Table 6.2). No parents abandoned their nests during this experiment, and all nestlings subjected to the fasting treatment fledged successfully.

Body Temperatures of Wild Nestlings

Body temperatures of 210 nestlings were measured on 26 dates in 1992 and 1993. Multiple regression of nestling body temperatures on air temperature, nestling age and an age by air temperature interaction explains a significant proportion of the variance in body temperature (Figure 6.9; overall adjusted $R^2 = 0.249$, p < 0.001; air temperature stand. coeff. = 0.728, p < 0.001; age stand. coeff. = 0.556, p = 0.024; interaction between air temperature and age stand. coeff. = -0.585, p = 0.045). Thus, the body temperatures of chicks are affected by their age and air temperature, and chicks of different ages respond differently to changes in air temperature.

Comparisons to Other Species

Data on changes in fat indices with age in several altricial species were gathered from published papers. Values were estimated from figures in all cases. Fat indices of 212 nestlings from 5 species of swallows

Table 6.1. Fasting capacity of tree swallows. Means (and standard deviations) are given for each age group. See text for methods and definitions.

Age	Avail. Fat (g)	Avail. Protein (g)	Total Reserves (kj)	RMR @30°C (kj/h)	RMR @20°C (kj/h)	Hours @30°C	Hours @20°C
3	0.02 (0.02)	0.003 (0.002)	2.02 (0.73)	0.15	0.05	13.5 (4.9)	42.9 (15.5)
6	0.19 (0.11)	0.004 (0.004)	10.61 (5.22)	0.59	0.50	17.9 (8.8)	21.1 (10.4)
9	0.62 (0.14)	0.051 (0.035)	29.53 (5.70)	1.17	1.17	25.2 (4.9)	25.2 (4.9)
12	0.81 (0.20)	0.122 (0.085)	38.02 (8.31)	1.26	2.07	30.3 (6.6)	18.4 (4.0)
15	1.51 (0.26)	0.237 (0.048)	65.68 (10.13)	1.53	1.89	43.0 (6.6)	34.8 (5.4)
F	0.88 (0.58)	0.244 (0.177)	40.21 (23.40)	1.59	2.40	25.3 (14.7)	16.8 (9.8)
A	1.17 (0.69)	0.378 (0.100)	51.00 (27.98)	1.59	2.40	32.1 (17.6)	21.3 (11.7)

Table 6.2. Mass loss of broods of tree swallow nestlings fasted at 20° and 30°C. Means \pm standard deviations are given. Differences between treatments in initial and final mass are not significant (ANOVA, initial: F = 0.19, p = 0.67; final: F = 3.25, p = 0.090). Differences in total mass lost and rate of mass loss are significant (ANOVA, mass lost: F = 68.93, p < 0.001; mass loss/hour: F = 74.01, p < 0.001).

Treatment	n	Initial mass (g)		Mass lost (g)	Mass loss/hour (g/h)
30°C	10	8.91 ± 1.59	7.82 ± 1.51	1.09 ± 0.16	0.10 ± 0.01
20°C	8	9.21 ± 1.26	8.96 ± 1.08	0.25 ± 0.27	0.02 ± 0.02

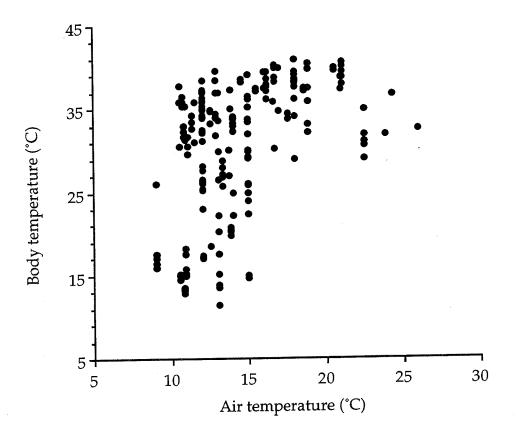
(Hirundinidae) tend to increase with age, while those of non-aerial insectivorous passerines (175 nestlings from four species) remain constant or show a slight decline (Figure 6.10). Nestling fat indices over all ages pooled are higher in passerine aerial insectivores (Table 6.3). Samples from both groups are equally distributed through the nestling period. The highest values for Fat Index in Figure 6.10 come from two studies on the house martin *Delichon urbica*. When values for this species are removed, the differences between Aerial and Non-Aerial insectivores are no longer significant (Table 6.3). Fat indices of non-passerine aerial insectivores are significantly greater than both aerial and non-aerial passerine insectivores (ANCOVA overall $R^2 = 0.20$, F = 56.31, p < 0.001, effect of category: p = 0.018; effect of age: p < 0.001).

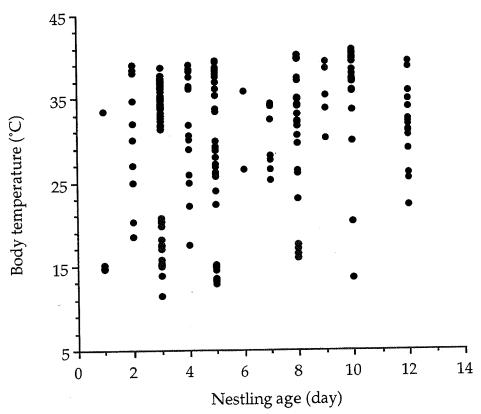
DISCUSSION

Fat content of nestling tree swallows increases steadily through the nestling periods, both in absolute terms and relative to the accumulation of non-lipid material. Eggs of tree swallows contain approximately 0.11 - 0.14 g of lipid (Shaw 1984, Ankley et al. 1993), suggesting that nestlings accumulate significant levels of fat reserves beginning around day 3, when nestlings contain an average of 0.08 ± 0.02 g of lipid. This increase in fat content was associated with an increase in the estimated fasting capacity throughout the nestling period.

Nestlings that died because of poor environmental conditions contained little fat, regardless of the age at which they died. The Fat Index of these nestlings tended to be lower in nestlings that died when they were older, indicating that older nestlings used up a greater proportion of their

Figure 6.9. Body temperature of nestling tree swallows in relation to air temperature and age. Multiple regression, overall $R^2 = 0.245$, p < 0.001, air temperature stand. coeff. = 0.476 p < 0.001, age stand. coeff. = 0.081, p = 0.19).





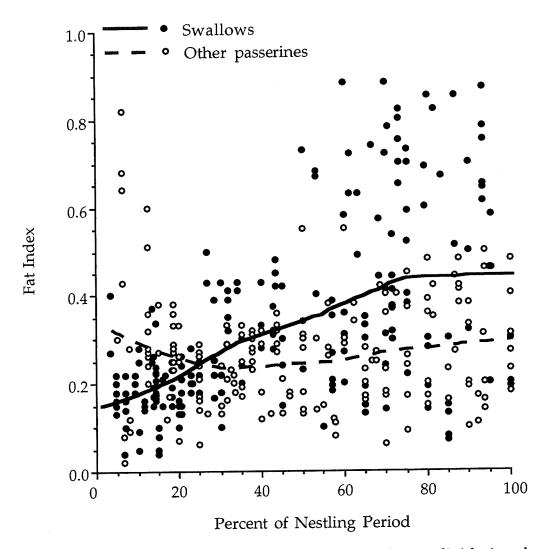


Figure 6.10. Changes in the Fat Index of swallows (Hirundinidae) and other insectivorous passerines. Swallows and older nestlings have significantly higher fat scores (ANCOVA overall R2 = 0.16, F = 36.0, p = 0.0001; effect of aerial versus non-aerial insectivore p = 0.0001, effect of age p = 0.0001; lines are LOWESS curves--Cleveland 1981). When *Delichon urbica* is excluded from the swallow category, there is no longer a significant effect of foraging habit (ANCOVA overall R2 = 0.07, F = 12.8, p = 0.0001; effect of aerial versus non-aerial insectivore p = 0.563, effect of age p = 0.0001). Species of aerial insectivores included and sources of data are: *Riparia riparia*, Turner and Bryant 1979; *Hirundo rustica*, Ricklefs 1967; *Hirundo tahitica*, Bryant and Hails 1983; *Delichon urbica*, O'Connor 1977a, Bryant and Gardiner 1979; *Tachycineta bicolor*, this study. Species of non-aerial insectivores included and sources of data are: *Agelaius phoeniceus*, Ricklefs 1967; *Parus caeruleus*, O'Connor 1977a; *Passer domesticus*, Blem 1975, O'Connor 1977a; *Campylorhynchus brunneicapillus*, Ricklefs 1975.

Table 6.3. Change in the Fat Index with age for nestlings of insectivorous birds. Ages are expressed both as percentage of the nestling period completed (Age, percent) and in absolute terms as the number of days since hatch (Age, days). Means (standard deviation) are given for each group, n = number of nestlings measured. Fat index and age (days) of swallows (Hirundinidae) are significantly higher than those of Non-aerial insectivores (ANOVA F = 12.55, p < 0.001, and F = 13.5, p < 0.001 respectively). Age (percent) does not differ (ANOVA F = 1.10, p = 0.30). Differences between means for Non-aerial insectivores and Aerial Insectivores with *Delichon urbica* excluded are not statistically significant (p = 0.91 for Fat Index, p = 0.09 for age, percent, and p = 0.14 for age, days). See Figure 6.10 for sources of data on passerines. Non-passerine aerial insectivores included are *Merops viridis* and *Collocalia esculenta*, Bryant and Hails 1983.

	Fat	Age,	Age,	n
	Index	percent	days	
Aerial Insectivores (=swallows)	0.33 (0.20)	0.46 (0.29)	10.5 (7.2)	212
Aerial Insectivores (Delichon excluded)	0.27 (0.15)	0.44 (0.29)	9.0 (5.8)	167
Non-passerine	0.51	0.65	22.3	65
Aerial Insectivores	(0.23)	(0.28)	(10.2)	
Non-Aerial	0.27	0.49	8.2	175
Insectivores	(0.13)	(0.28)	(4.9)	

energy stores before death. These nestlings had also ceased growing and developing when the environmental conditions deteriorated. All of the measures of growth and development, including tarsus, wing and feather length, and body mass, show significant reductions in dead nestlings. This result is supported by the patterns of non-lethal effects of the environment on growth discussed in Chapter Seven. The internal organs of dead nestlings show a similar decrease in absolute growth, and the relative sizes of these organs at death suggest that these reductions although smaller for internal organs, are spread across all body components (Figure 6.4).

Fasting birds use fat as their primary energy source, switching to protein metabolism only after most or all of the available lipids are metabolized (Pope and Ward 1972, Houston 1977, Blem 1990). Although glycogen and carbohydrate stores do fuel metabolism, they are not generally considered to be significant sources of energy for fasting birds (Farner et al. 1961, Blem 1990). Assuming that the pectoralis muscles are the primary source of protein stores (Grammeltvedt 1978, Zazula 1984), it is apparent from both the absolute and relative mass of the pectoralis of dead nestlings that some protein metabolism had occurred before death in older nestlings. The muscles that make up the remaining portion of the body (empty body mass) show no decline in dead nestlings, supporting the assumption that the pectoralis muscles are the primary source of protein.

The reduction in relative size of the pectoralis and in fat stores suggests starvation as the mechanism of mortality in the dead nesting sample. The fat contents of dead nestlings (equal to approximately 0.02 g / g wet mass) are similar to those found in adult birds that had starved to death (Zimmerman 1965, Ward 1969, Pope and Ward 1972, Marcström and

Mascher 1979). Water content of dead nestlings showed no decline, indicating that dehydration did not play a role in these deaths. Neither organ mass nor the visual inspection of organs during dissection showed any abnormalities. The possibility that hypothermia played some role in these deaths cannot be eliminated. Based on the results of the fasting experiment and the profile of nestling body temperatures discussed below, however, it appears that nestling tree swallows are quite resistant to low body temperatures and that hypothermia alone is not a likely cause of death.

The values for the various components of body composition of fledglings and adults show that considerable development occurs after day 15 in tree swallows (Figures 6.5 and 6.6). The few significant differences between healthy and dead fledglings and adults results from the greater variability in the values for those individuals, relative to chicks. This variability is probably due to the more diverse conditions under which those individuals died, making my categories of healthy and dead overly simplistic. For example, some adults from both categories had fat levels below the starvation threshold of 0.02 g fat / g lean dry mass, suggesting that some individuals found dead in nest boxes may have died of disease or hypothermia, and that some adults hit by cars while foraging over roads may have been nutritionally stressed. Although this variability makes it difficult to detect differences between the categories I used, it does reflect real variability present in the population, and the mean values provide a useful comparison when looking at the development of nestlings.

Fledglings will also be subject to unpredictable changes in conditions and postfledging survival is associated with nestling mass and size

(Chapter Five). However, the lack of correlation between fat content and any measures of body size or mass of day 12 and 15 nestlings suggests that the mechanism behind this relationship between nestling body mass and size and postfledging survival is not related to larger and heavier nestlings having extra energy reserves (Garnett 1981, Thompson et al. 1993).

Short-term fluctuations in environmental conditions leading to nestling starvation are an important source of reproductive failure in tree swallows, a pattern observed in several other groups of aerial insectivores (Edson 1943, Koskimies 1950, Lack and Lack 1951, Wrege and Emlen 1991, Hill and Chambers 1992). In this population, mortality of nestlings reaches 50 - 60 % in some years, significantly reducing the breeding population. The intensity and frequency of these cases of reproductive failure suggest that there is the potential for strong selection for traits that would buffer these species from the effects of poor environmental conditions. One prediction would be that aerial insectivores should have higher fat stores than non-aerial insectivores. Changes in Lipid Index with age are available for several species of passerines and show that, while fat stores in the swallows as a group are generally higher than in other insectivorous passerines (Figure 6.10 and Table 6.3), these differences are due to the high fat stores found in the house martin, Delichon urbica (Table 6.3). Although this suggests that most swallow species, including tree swallows, are not sequestering unusually large fat stores, the high levels of fat in nestlings of Delichon urbica and in non-passerine aerial insectivores (Table 6.3) suggests that this strategy may be used in other species. These data may also shed some light on the debate about the high fat content found in nestlings of Procellariiform sea birds (Ricklefs et al. 1980, Ricklefs

and Schew 1994). The high fat reserves in nestling petrels could function either as insurance against short-term periods of poor feeding conditions (Lack 1968, Ricklefs and Schew 1994) or their primary function could be to act as an energy sink to compensate for a diet high in fat but low in nutrients (Ricklefs et al. 1980, see also Thomas et al. 1993). Since the high energy reserves of aerial insectivores are not needed as an energy sink (since insects have a relatively high protein content), and presumably function as insurance, the possibility that fat also functions as insurance energy in petrels cannot be eliminated.

A second strategy that could be used to buffer nestlings from periods without food is to decrease energy use, thereby increasing the length of time that nestlings can survive with their available reserves. In homeothermic nestlings, this could be accomplished by parents sacrificing some of their energy reserves to brood offspring, decreasing the energy nestlings need to put into thermoregulation (Chapter Four). Alternatively, the costs of thermoregulation could be saved through the use of torpor (Heller 1988, Ricklefs 1988). The energy demands of nestling tree swallows drop dramatically with a decrease in body temperature (Chapter Four) and could be interpreted as a form of torpor.

The estimates of fasting capacity presented here suggest that, in younger tree swallows, survival time could be greatly increased if parents do not attempt to brood their offspring (Table 6.1). The results of the fasting experiment support this result. Nestlings with moderate abilities to thermoregulate lost mass at a rate similar to that of fasting adults of other species (Kendeigh 1945). Day 6 nestlings had lower body temperatures and lost less mass at lower ambient temperatures. The opposite pattern would

be expected in older nestlings, unless their body temperatures dropped. Results of experiments by Baldwin and Kendeigh (1932) support this hypothesis. They found nestling house wrens (*Troglodytes aedon*) younger than six days survived longer at lower ambient temperatures, and that the situation was reversed in older nestlings, as is predicted by my estimates of fasting capacity (Table 6.1). My estimates of survival time almost certainly underestimate survival ability (cf. Brenner and Malin 1965), both because fasted birds undergo a series of metabolic and behavioral changes that act to prolong survival (Ivacic and Labisky 1973, Biebach 1977, Ketterson and King 1977, Cherel et al. 1988) and because parents do provide some food during adverse weather (McCarty unpublished).

Although nestlings of many species are known to be capable of surviving at low body temperatures for extended periods of time (Baldwin and Kendeigh 1932; Dawson and Evans 1960; Hill and Beaver 1982; Magrath 1988; Prinzinger and Siedle 1986, 1988; Clum 1991; Olson 1992), the occurrence of prolonged low body temperature in nestling passerines has generally been regarded as a pathological condition. Nestlings of another swallow species (*Delichon urbica*) are known to be capable of undergoing torpor (Prinzinger and Siedle 1986, 1988) and torpor has been observed in adults of the congeneric violet-green swallow (*Tachycineta thalassina*; Lasiewski 1966). Additional physiological data would be required to conclude that the observed reductions in body temperature of nestling tree swallows represent torpor in the sense of a controlled reduction in temperature. It is clear that even if these body temperature reductions are solely under the control of the parents, the result is the same as that of

torpor. The correlation between low food availability and low ambient temperatures (Chapter Seven) increases the potential importance of torpor or torpor-like effects for tree swallows.

Although the results of the fasting experiments suggest that reductions in nestling body temperature could be used as a strategy for prolonging survival, it is not known if tree swallows actually employ this strategy during periods of low food availability. Measurements of nestling body temperature in the field during periods of poor environmental conditions do show significant reductions in body temperature in some individuals. Although these reductions are most pronounced in young nestlings, nestlings above the age of effective homeothermy (about 5 - 6 days; Dunn 1979) also showed reduced body temperatures. These measurements do not distinguish between the use of torpor as a strategy and the simple inability of parents and nestlings to maintain high nestling body temperatures, however, they do suggest that reduced body temperatures may contribute to energy savings in wild tree swallows.

Similarly, the delay of growth and development in fasting nestlings (see also Chapter Five) will result in significant energy savings and presumably prolonged survival during periods of adverse environmental conditions (O'Connor 1977b, Emlen et al. 1991). Although this result is consistent with the hypothesis that delayed growth and development is an adaptive strategy to increase survival during short-term environmental fluctuations, the alternative that delayed growth and development are incidental results of decreased body temperature and nutrient limitations is equally likely.

Distinguishing between the adaptive and non-adaptive explanations for decreased body temperature and delayed growth and development in tree swallows and other species subject to short-term fluctuations in food supply will require data on the abilities of related species from less variable environments to undergo these adjustments (Emlen et al. 1991). If it were shown that species from less variable environments are also able to survive low body temperatures and to delay growth and development, this would suggest that these characteristics in aerial insectivores are not adaptations for prolonging survival during short-term fluctuations in food supply. Instead, this would suggest that these abilities are common to most altricial birds and, although useful to aerial insectivores, not a result of evolutionary response to the strong short-term variability in food supply they experience. The lack of published observations from non-aerial insectivorous species cannot be seen as evidence in support of the adaptive nature of these phenomena since one would predict that, all other things being equal, reductions in body temperature, growth, and development will be observed most frequently in those species most frequently exposed to short-term deterioration in environmental conditions.

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CHAPTER SEVEN:

Relative Importance of Environmental Variables in Determining the Growth of Nestling Tree Swallows

INTRODUCTION

Environmental fluctuations on a variety of temporal and spatial scales have profound effects on both the growth and survival of nestling tree swallows (*Tachycineta bicolor*; Chapters Five and Six). In this chapter, I will investigate the relative importance of different components of the environment on nestling growth. Nestling growth rates are an appropriate indicator of the effects of environmental variation on fitness because growth varies on the same short time scale as environmental conditions, and because growth has been shown to be a good indicator of subsequent survival and reproductive success of tree swallows (see Chapter Five) and a variety of other species (Perrins 1965, 1988; Dhondt 1979; Garnett 1981; Nur 1984; Davies 1986; McGowan 1987; Gustafsson and Sutherland 1988; Tinbergen and Boerlijst 1990; Gebhardt-Heinrich and van Noordwijk 1991; Magrath 1991; Lindén et al. 1992).

Changes in environmental conditions during the breeding season are an important component of variation in reproductive success in birds, influencing clutch size, timing of breeding, and nestling growth and survival (Lack 1954; Van Balen 1973; O'Connor and Morgan 1982; Murphy 1983, 1985; Järvinen 1989; Brawn 1991; Rotenberry and Wiens 1991). Environmental effects are especially dramatic in groups of birds whose food supply fluctuates unpredictably over a short time period, notably seabirds (e.g. Hawksley 1957, Dunn 1975, Konarzewski and Taylor 1989, Becker and Specht 1991) and aerial insectivores such as swallows, swifts, and beeeaters (Chapter Five; Edson 1943; Koskimies 1950; Lack and Lack 1951;

Gladwin and Nau 1964; Elkins and Etheridge 1974; Bryant 1975, 1978; O'Connor 1979; Wrege and Emlen 1991; Hill and Chambers 1992). Environmentally induced fluctuations in reproductive success in turn can influence other aspects of avian life histories (Partridge and Harvey 1988) and subsequent population size (Chapter Five, Wiens 1974, Järvinen 1989).

Given the potential for selection due to environmental variability, one would predict that organisms subject to frequent and severe environmental fluctuations would evolve strategies to buffer themselves from such changes. However, the predicted responses of breeding birds to environmental changes are still ambiguous. If we are to attempt to make predictions about potential responses to environmental selection pressures, we need to specify the scale on which variation occurs and know more about the relative importance of the various environmental components. The spatial and temporal scale of fluctuations will determine the possible strategies that could be employed by individuals to buffer themselves from the effects of environmental variability. For example, the use of habitat selection, brood reduction, clutch size adjustments, or torpor would each be appropriate for different scales of variability (c.f. O'Connor 1977, Brawn 1991, Rotenberry and Wiens 1991). Although environmental variation on a variety of scales is known to influence the growth of nestling tree swallows (see Chapter Five), this analysis will focus on short-term temporal variations in food and weather.

In addition to the scale of the variability, information about the nature of the variation is also required before predictions about potential responses can be made. For example, reductions in nestling growth can be either due to a direct reduction in the availability of food or, alternatively,

due to an increase in energetic demands due to changes in ambient temperature. In the first case an appropriate reaction by the parents could be to devote a greater proportion of the time budget to foraging, while in the second case the appropriate adjustment may be to forgo foraging in favor of increased brooding. The importance of these factors can change depending on the stage of the reproductive season (Clark and Ricklefs 1988). Dramatic changes in energy requirements and tolerance to environmental conditions (which are expected to influence responses to environmental variation) occur during the growth and development of altricial nestlings.

Food supply has been assumed by many to be the most critical environmental variable in determining the success of adult birds at raising young (Lack 1947, 1968; Drent and Daan 1980; Newton 1980; Quinney et al. 1986; Martin 1987, 1992). Support for this view comes from the frequency of starvation of offspring, especially in species that undergo frequent brood reduction or that are dependent on food supplies subject to short-term fluctuations (Ricklefs 1969). Results of food supplementation experiments, where individuals provided with extra food tend to raise heavier or more offspring (e.g. Högstedt 1981, Arcese and Smith 1988, Smith and Arcese 1988, Simons and Martin 1990, Richner 1992, Nilsson 1994) also support the view that food is an important limit on reproduction in birds. It is clear, however, that food is not always limiting (cf. Newton 1980), and the views of many ornithologists, especially some of those that study temperate-zone bird communities, is that food is rarely limiting during the breeding season and is in fact super-abundant during nesting (e.g. Wiens 1973, 1974, 1977; Rotenberry 1980).

Few studies have simultaneously examined the effects of food supply and other environmental factors, such as ambient temperature, rain, and wind, that could influence nestling success (but see Lack and Lack 1951, Bryant 1975, Slagsvold 1976, O'Connor 1978, Zammuto et al. 1981, Yom-Tov and Wright 1993). Such an analysis is complicated by the correlation that often exists between food and other environmental factors. To address this problem, I will use the method of path analysis, which was developed to examine the relative effects of correlated independent variables and can be used to compare alternative models describing relationships among variables (Sokal and Rohlf 1981, Pedhazur 1982, Kingsolver and Schemske 1991, Wootton 1994). In particular, I will; 1) compare the relative importance of food supply, ambient temperature and other weather variables in determining growth in nestling mass, 2) determine how the relative importances of these factors change with nestling age and development, and 3) examine the importance of environmental factors in determining the structural growth of nestling flight feathers.

METHODS

Tree swallows breeding in nest-boxes were studied at the Cornell University Experimental Ponds Facility (42° 30' N; 76° 27' W), near Ithaca, New York. This facility consists of two breeding sites located approximately 2 km apart. Unit One consists of approximately 55 - 75 pairs of breeding tree swallows, and Unit Two has between 10 and 23 pairs. Swallows breeding at these sites are monitored closely for the exact date of hatching to determine nestling age: nestling ages are given as hatch day =

nestling day 1. Nestlings were weighed to the nearest 0.1 g during the 1990 - 1993 breeding seasons using either Pesola spring scales or a portable O'Haus electronic balance. Length of the ninth primary was measured to the nearest 0.5 mm on days 10 and 12 in 1992 and 1993.

Growth rate was defined as the change in mass (or feather length) between two measurements approximately 48 hours apart. Environmental data from the intervening day were used in the path analysis. The mean change for all the nestlings in a brood was used in the analyses to avoid any possible effects of non-independence among nestlings within a brood. Each brood appears no more than once in each path diagram, but some broods were used in more than one path diagram (e.g. as young and as old nestlings).

Environmental variables were measured at the Unit One site. Insect abundance was measured using a 12 m Rothamsted Insect Survey suction trap (Macaulay et al 1988). This trap provides an excellent index of the abundances of flying insects found at the heights most frequently used by foraging tree swallows (Chapter Two and Appendix One). Large numbers of thrips (Order Thysanoptera) occasionally occur in the suction trap samples, however due to the small size of thrips (usually < 0.5 mm) and the fact that they were never observed in the swallow diets (Chapter Two), all subsequent analyses exclude thrips. Numbers of insects captured were converted into mass of insects per hour of sampling using the conversions described in Chapter Two. Insect abundances were then log-transformed to meet the linearity assumption of the path analyses described below.

Weather variables measured included temperature, rain, and windspeed. Data were recorded in the morning (0600 - 0730) and again later in

the day (1700 - 1900). With the exception of minimum temperature, which usually occurred in the night, all variables refer to the conditions during daylight hours (i.e. rain recorded during the night is not included in these analyses). Significant rainfall occurred on less than a third of the days during the nestling period and was not statistically well behaved. For this reason, rain was excluded from the path analyses and the effects of rain on growth were analyzed separately, treating rain as a categorical variable. Since more than one brood may have been measured on any given day, dates, and their associated environmental data, may appear more than once in each path diagram.

Path Analysis

Path analysis was developed by Sewall Wright (Wright 1920) as a method for interpreting the causal relationships among a set of correlated variables. Working in the context of an *a priori* model of causal relationships, path analysis provides information on both the relative importance of the independent variables and an indication of the fit of the model to the data. Although not a replacement for experiments, path analysis is a powerful tool for interpreting observational data and testing hypotheses, especially in systems where experiments are not feasible (Sokal and Rohlf 1981, Pedhazur 1982, Schemske and Horvitz 1988, Mitchell 1992). Path analysis has recently been applied to a wide range of questions in ecology and evolutionary biology including studies of pollination biology and reproductive success of both plants and animals (Schemske and Horvitz 1988, Stanton et al. 1991, Forslund and Larsson 1992, Mitchell

1994), measurement of natural selection (Crespi and Bookstein 1989, Crespi 1990), and community ecology (Kohn and Walsh 1994, Wootton 1994).

Path diagrams provide several types of information. The diagrams presented here follow the conventions of Kingsolver and Schemske (1991) and Mitchell (1992). Lines with a single arrow imply an *a priori* causal relationship in the direction indicated; double-headed arrows imply correlation with no causality assumed. Solid lines indicated positive relationships and dashed lines negative relationships. The strength of the relationship as determined by the standardized path coefficient is indicated by the width of the line. The statistical significance of individual path coefficients is indicated by asterisks. No asterisk indicates $p \ge 0.10$, indicates $p \ge 0.10$, indicates $p \ge 0.01$, and indicates $p \ge 0.01$. Residual or error variables, denoted by $p \ge 0.01$, and indicates $p \ge 0.01$. Residual or error variables, denoted by $p \ge 0.01$, represent the total effect of all unmeasured variables on the dependent variable $p \ge 0.01$. Mitchell 1992).

Hypotheses Tested

The basic hypothesis tested (Figure 7.1) proposes that increases in ambient temperature and food supply cause faster nestling growth. Higher temperature should also indirectly increase growth by increasing the abundance of insects. Wind is proposed to decrease parental foraging efficiency leading to a decrease in growth rate. Wind is also expected to have an indirect negative effect on growth by decreasing the numbers of insects in the air column (Freeman 1945, Williams 1961, Schaefer et al. 1985, Pitcairn et al. 1990). Hatch date of the chicks is included in the path

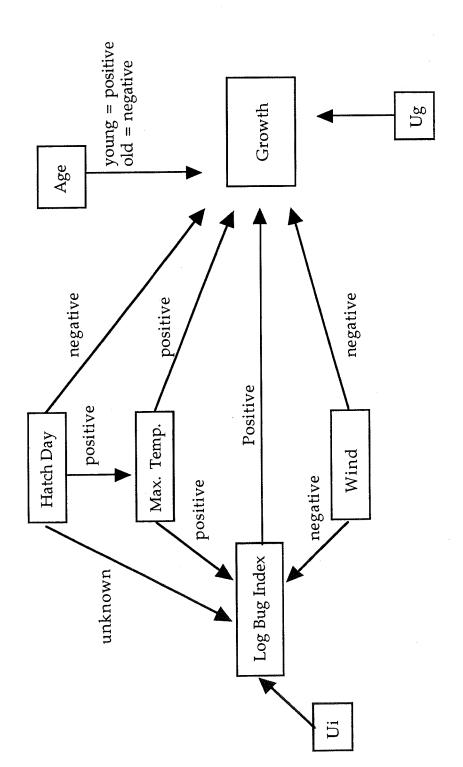


Figure 7.1. Path diagram of the a priori hypothesis of the relationships of environmental variables to nestling growth.

diagram to control for the observed changes in reproductive success associated with season (von Haartman 1966, Stutchbury and Robertson 1988, Hochachka 1990, D. W. Winkler and P. Allen unpublished data). Age is included in some path diagrams to control for the effect of age on growth within a given age category. The age category of "young nestlings" includes nestling growth on days 2, 3, and 4, while "old nestlings" include days 9, 10, and 11. The young age category consists of nestlings prior to the onset of significant thermoregulatory ability, while the old nestlings are capable of thermoregulation (Dunn 1979, Marsh 1980). Nestlings older than day 12 were not used because they show no consistent change in mass. The hypothesis that age influences the relative importance of different environmental variables is tested by comparing path diagrams for young nestlings to those of old nestlings. The consistency of the results of the path analysis are examined by performing the same analysis on data from different years and age categories of chicks.

The effect of brood size is not included in the basic path diagram (Figure 7.1) but was analyzed separately using the hypothesis that brood size and hatch day each have direct effects on growth and hatch day in turn affects brood size. If brood size is adjusted to the level that parents can successfully raise during normal environmental conditions, a negative effect of brood size on growth should be most pronounced on days with little food available. This was tested using the same hypothesis as above using only data from days where the Bug Index was below the median level.

Growth of the ninth primary feathers between days 10 and 12 was examined using the hypothesis analogous to the one in Figure 7.1.

Nestling tree swallows are capable of sustained flight before they fledge (pers. obs.), and development of flight feathers is a critical component of their development. The analysis of growth of structures such as feathers differs from mass increase because feather growth involves not only the accumulation of biomass but the synthesis and differentiation of a complex structure. For this reason, feather growth may be relatively immune to environmental effects on the day of growth and could be influenced by environmental conditions prior to the actual growth. This hypothesis was tested using a path diagram that included insect abundances from the day of growth (day 11) and the four preceding days (nestling days 7 - 10).

As discussed above, dates may appear more than once in each path diagram. Although this poses no problem for the paths leading to the dependent variable (growth rate), it may make the interpretation of paths among environmental variables difficult. This possibility that path coefficients were biased was tested by constructing a separate path diagram of environmental variables, based on all of the environmental data available for days 25 - 55 in all four years. These paths were then compared to the patterns seen in the path diagrams based on the hypothesis in Figure 7.1.

RESULTS

Environmental Conditions

Weather conditions varied dramatically on a daily basis during the times that tree swallows were raising offspring (Figure 7.2). Although significant seasonal trends are found in most years (see below), the day-to-day changes far outweigh the longer term changes in environmental

conditions. The abundances of aerial insects show the most dramatic daily changes, with variation across three to four orders of magnitude being observed in the span of a few days (Figure 7.3). Insect abundances show an increase through the nestling season in three of four years; however, this relationship is weak and significant only in 1993 ($R^2 = 0.16$, p = 0.04, slope = 0.031).

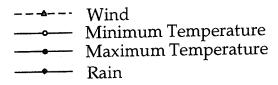
Environmental conditions also varied among years (Table 7.1). Minimum and maximum temperature, as well as insect abundances showed significant between-year effects, with 1992 and 1993 being colder and having lower levels of available insects than 1990 and 1991 (Table 7.1). Wind speeds and rainfall did not differ significantly among years (Table 7.1).

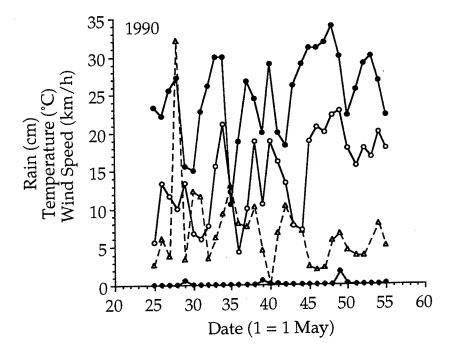
Environmental Effects on Mass Change

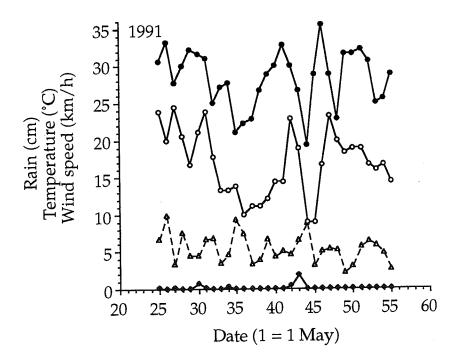
The correlation matrix for the environmental variables from Figure 7.1 show that the relationships generally match the predictions that nestlings should grow faster on warm days with high levels of available insects (Table 7.2). However, the strong correlations among some of the variables (e.g. food supply and temperature) emphasize the need to use path analysis for this system.

The path diagram for young nestlings in all years pooled shows that the most important of the hypothesized environmental variables influencing growth is maximum ambient temperature, which has a strong positive effect on growth (Figure 7.4a). Time of year has a direct negative effect on nestling growth, independent of any seasonal changes in

Figure 7.2. Variation in weather conditions during the nestling phase of the tree swallow breeding season, 1990 - 1993.







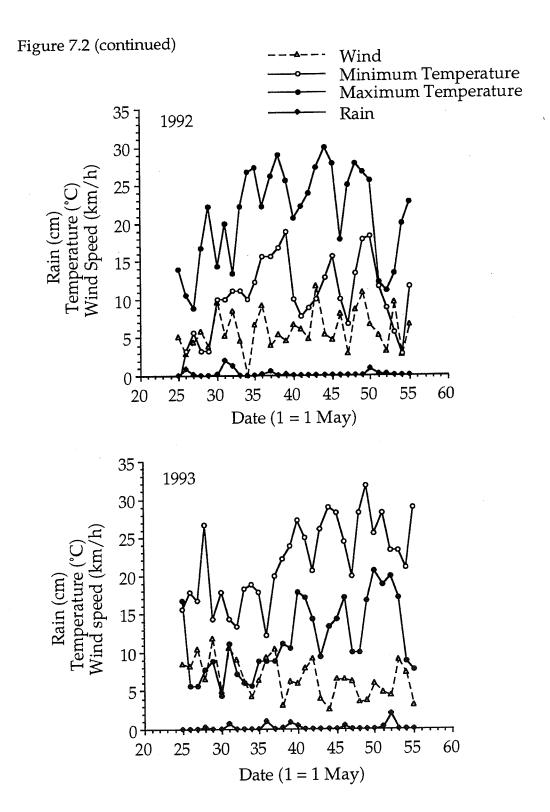


Figure 7.3. Variation in the abundance of aerial insects during the nestling phase of the tree swallow breeding season, 1990 - 1993.

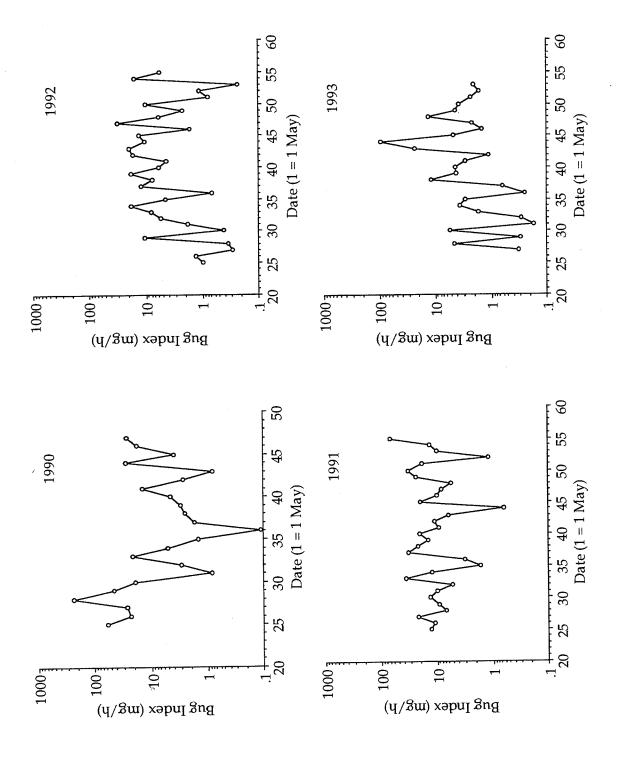


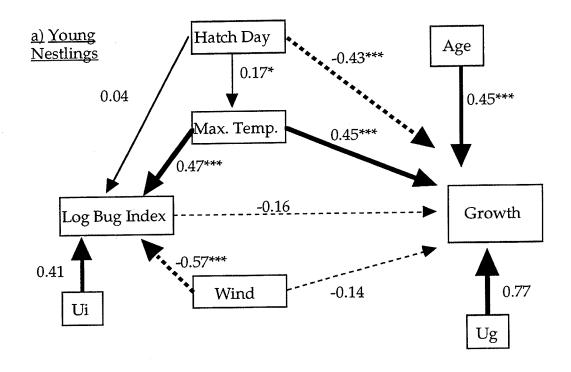
Table 7.1. Variation among years in environmental variables. Data from day 25 (25 May) through day 55 (24 June). F and p-values from ANOVA given for each environmental variable. Mean (standard deviation) given for each year. Wind = average wind speed (km/h), Min. T. = minimum temperature (°C), Max. T. = maximum temperature (°C), Rain = average daily rainfall (mm), Log B. I. = log of Bug Index (Log mg insects / hour).

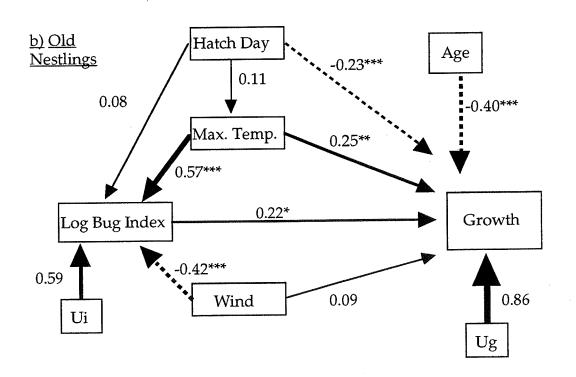
	Wind	Min. Temp.	Max. Temp.	Rain	Log B.I.
F	1.33	10.65	12.00	0.47	6.22
p - value	0.27	< 0.001	< 0.001	0.70	<0.001
1990	7.0 (5.7)	14.2 (5.5)	25.0 (5.5)	0.11 (0.32)	0.85 (0.75)
1991	5.4 (1.9)	16.8 (4.5)	28.4 (3.9)	0.12 (0.37)	1.02 (0.44)
1992	5.9 (2.6)	10.2 (5.0)	21.1 (6.2)	0.20 (0.45)	0.58 (0.62)
1993	6.6 (2.5)	11.7 (4.8)	22.0 (5.3)	0.19 (0.41)	0.38 (0.63)

Table 7.2. Correlation matrix for the variables used to test the hypothesis shown in Figure 7.1. Data from 1990 - 1993. Correlations for young nestlings shown above the diagonal, correlations for old nestlings given below the diagonal. Change = change in nestling mass, Hatch = hatch day, Age = age of brood, Max. T. = maximum temperature, wind = average wind speed, Log B. I. = log of Bug Index (Log mg insects / hour).

	Change	Hatch	Age	Max. T.	Wind	Log B.I.
Change	-	-0.30	0.36	0.26	-0.11	0.15
Hatch	-0.16	-	0.09	0.21	-0.24	0.28
Age	-0.29	-0.03		-0.11	0.05	-0.06
Max. T.	0.25	0.11	0.26	-	-0.48	0.76
Wind	-0.04	-0.19	-0.03	-0.23	-	-0.81
Log B.I.	0.23	0.22	0.15	0.68	-0.57	### APP

Figure 7.4. Path diagram showing the effects of environmental variables on growth of young and old nestling tree swallows. "Young" nestlings includes growth of nestlings on days 2, 3, and 4; "old" nestlings includes nestling growth on days 9, 10, and 11. Solid lines indicate positive path coefficients, while dashed lines indicate negative path coefficients. Statistical significance of individual path coefficients is indicated by asterisks: * indicates $0.10 > p \ge 0.05$, ** indicates $0.05 > p \ge 0.01$, and *** indicates p < 0.01. The model for young nestlings (Figure 7.4a) includes 125 broods and has $R^2 = 0.40$, p < 0.001 for growth and $R^2 = 0.83$, p < 0.001 for Log Bug Index. The model for old nestlings (Figure 7.4b) includes 143 broods and has $R^2 = 0.26$, p < 0.001 for growth and $R^2 = 0.65$, p < 0.001 for Log Bug Index.





temperature or food supply. Wind and log Bug Index show small, non-significant effects. A slight tendency for temperature to increase later in the season is evident in these path diagrams. Such an increase in temperature would in turn act to reduce the magnitude of the overall effect of season on growth. Variation in insect abundance is explained to a large extent by wind and temperature (Figure 7.4a). The positive effect of age on growth is as expected, reflecting the increase in growth rate seen in young nestlings (see Chapter Five).

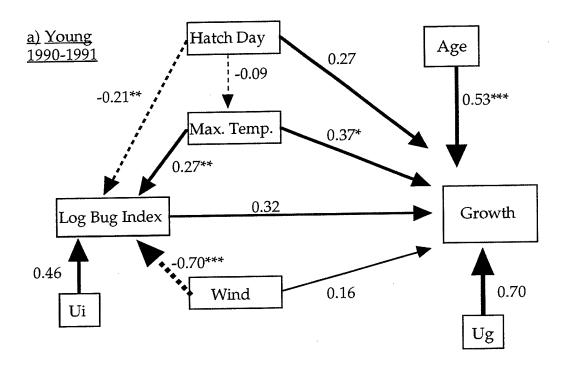
For nestlings old age category, pooled across years, the hypothesis results in a similar pattern, except for the increase in the importance of insect abundance in explaining growth (Figure 7.4b). Based on this path diagram, it appears that food and temperature have equally strong direct effects on growth for older nestlings. However, temperature has an additional, indirect effect on growth through its positive effect on food. The effect of season on growth is weak. Growth rates of nestlings in this age group are decreasing, resulting in the negative path coefficient for age within the age category (see Chapter Five).

Subsets of the data sets from Figure 7.4 were examined to determine the generality of the patterns. Young nestlings were divided into four data sets. Young nestlings from 1990 and 1991 were pooled to provide sufficient sample size (Figure 7.5a). The most significant difference in this path is that nestlings actually grew better later in the season, and food supply was more important (although its coefficient was still not significant). Young nestlings from 1992 (Figure 7.5b) had slower growth later in the season, but the food supply had a strong positive effect. The effect of maximum temperature is considerably lower than for the pooled data, and wind

emerges with a strong direct positive effect on growth. Young nestlings in 1993 were measured both between days 1 and 3 and between days 3 and 5. The path diagram explains a trivial amount of the variation in growth for nestlings measured between days 1 and 3 (Figure 7.6a) and none of the environmental variables shows a significant effect. This is not simply a result of relatively small sample size (45 broods), since much of the variability in insect abundance is explained. For growth between days 3 - 5 maximum temperature emerges as having a strong effect on growth, while insect abundance has a negative path coefficient (Figure 7.6b). There is no effect of season except for an indirect effect due to the increase in maximum temperature with season.

Older nestlings were divided into five subsets to examine the consistency among years of the patterns observed in Figure 7.4a. Broods from 1990 and 1991 were pooled to provide sufficient sample size. For 1990-1991 the multiple regression of growth was not significant, resulting in non-significant path coefficients (Figure 7.7). Nestlings in 1992 and 1993 were divided into 8 - 10 and 10 - 12 day old categories. In both 1992 (Figure 7.8a) and 1993 (Figure 7.8b) nestling growth between days 10 - 12 shows similar patterns. Growth decreases through the season and both temperature and food supply show positive effects on growth. Wind shows a negative direct effect in 1992 and a positive effect in 1993. Food, temperature, and date were more important in 1993. Paths for day 8-10 nestlings show a strong effect of temperature in 1992 (Figure 7.9a) and of temperature and date in 1993 (Figure 7.9b).

Figure 7.5. Path diagram showing the effects of environmental variables on growth of young nestling tree swallows in 1990 - 1991 and 1992. The pooled data for 1990 and 1991 (Figure 7.5a) includes 33 broods and has $R^2 = 0.51$, p = 0.001 for growth and $R^2 = 0.79$, p < 0.001 for Log Bug Index. The model for 1992 (Figure 7.5b) includes 19 broods and has $R^2 = 0.69$, p = 0.005 for growth and $R^2 = 0.96$, p < 0.001 for Log Bug Index. See figure legend for Figure 7.4 for definitions and conventions.



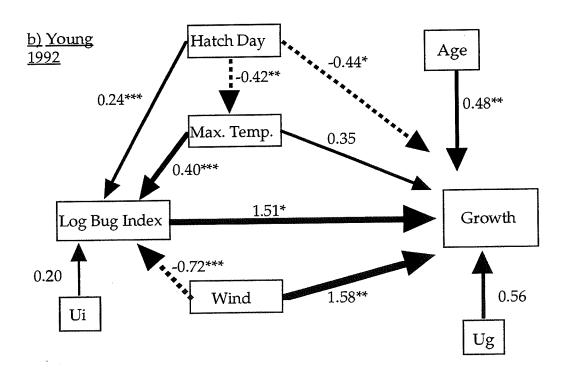
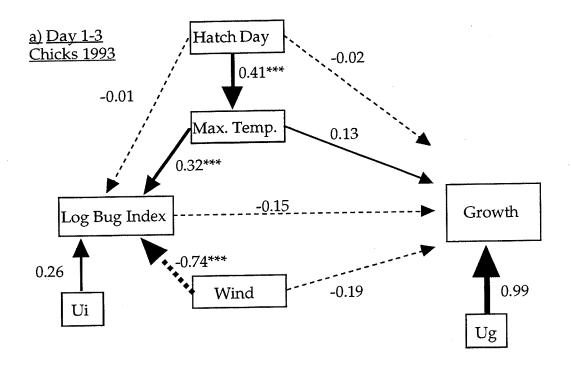
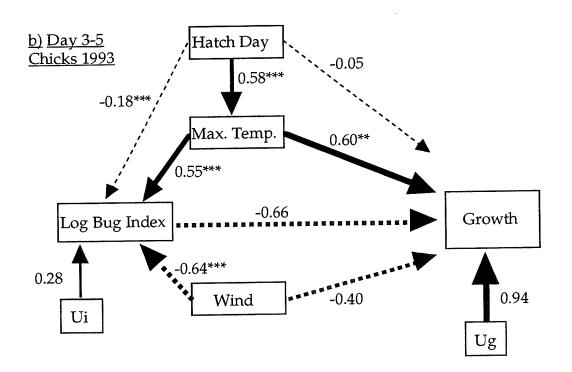


Figure 7.6. Path diagram showing the effects of environmental variables on growth of nestling tree swallows between days 1 and 3 and between days 3 and 5 in 1993. Data from 45 broods between days 1 and 3 (Figure 7.6a) give $R^2 = 0.02$, p = 0.92 for growth and $R^2 = 0.93$, p < 0.001 for Log Bug Index. Day 3 - 5 nestlings (Figure 7.6a) include 66 broods and give $R^2 = 0.12$, p = 0.11 for growth and $R^2 = 0.92$, p < 0.001 for Log Bug Index. See figure legend for Figure 7.4 for definitions and conventions.





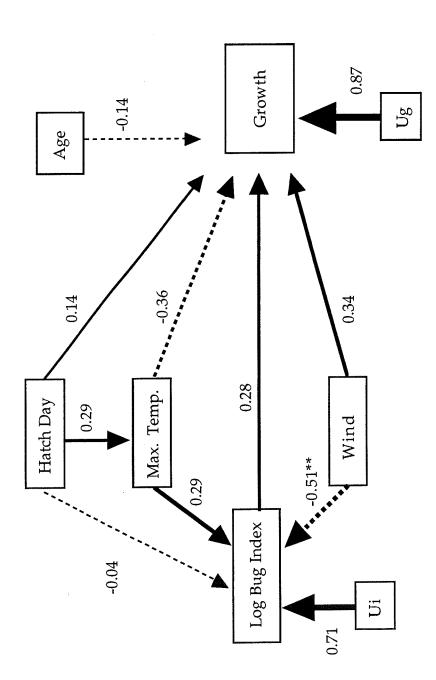
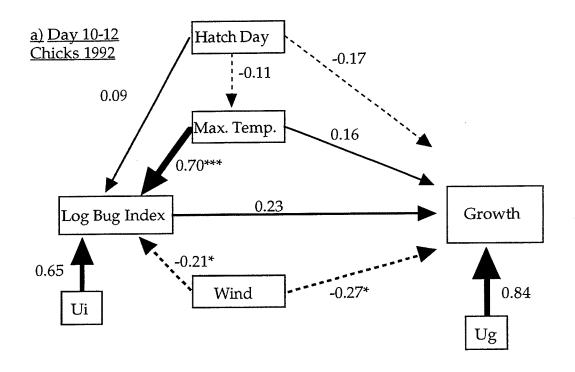


Figure 7.7. Path diagram showing the effects of environmental variables on growth of old nestling tree swallows in 1990 - 1991. Model includes 25 broods and has an \mathbb{R}^2 = 0.24, p = 0.35 for growth and $R^2 = 0.49$, p = 0.002 for Log Bug Index. See figure legend for Figure 7.4 for definitions and conventions.

Figure 7.8. Path diagram showing the effects of environmental variables on growth of nestling tree swallows between days 10 and 12 in 1992 and 1993. In 1992 (Figure 7.8a) the model includes 40 broods and has an R^2 = 0.29, p = 0.016 for growth and R^2 = 0.58, p < 0.001 for Log Bug Index. In 1993 (Figure 7.8b) the model includes 59 broods and has an R^2 = 0.30, p < 0.001 for growth and R^2 = 0.86, p < 0.001 for Log Bug Index. See figure legend for Figure 7.4 for definitions and conventions.



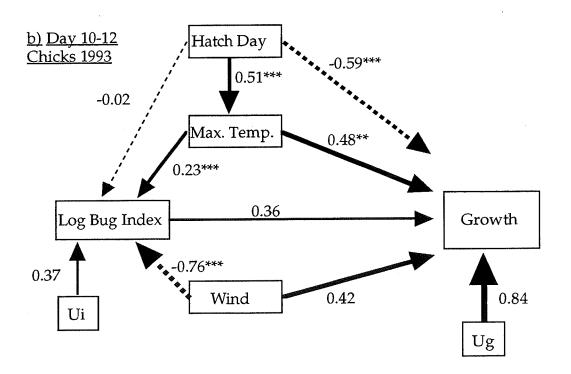
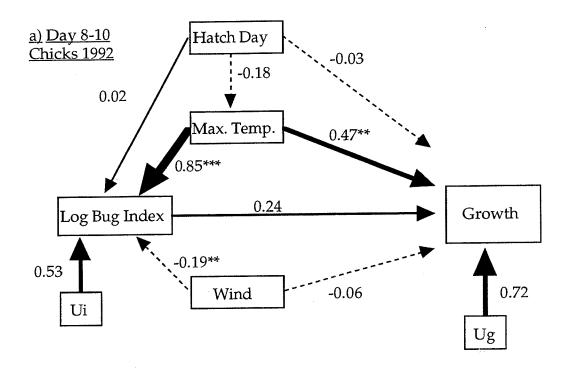
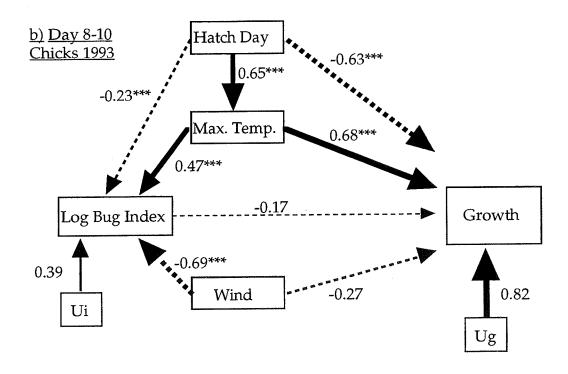


Figure 7.9. Path diagram showing the effects of environmental variables on growth of nestling tree swallows between days 8 and 10 in 1992 and 1993. In 1992 (Figure 7.9a) the model includes 54 broods and has an R^2 = 0.48, p < 0.001 for growth and R^2 = 0.72, p < 0.001 for Log Bug Index. In 1993 (Figure 7.9b) the model includes 63 broods and has an R^2 = 0.33, p < 0.001 for growth and R^2 = 0.85, p < 0.001 for Log Bug Index. See figure legend for Figure 7.4 for definitions and conventions.





The consistency of the relationships among variables in different years is summarized in Table 7.3. All of the diagrams for young nestlings support the positive effect of ambient temperature on growth seen for the pooled data (Table 7.3). The lack of an effect of food supply on young nestlings (Figure 7.4a) appears to be the result of variable importance of insect abundance in different years, with 2 data sets producing positive path coefficients and two negative (Table 7.3). Similarly the weak effect of wind seen is the result of two positive and two negative coefficients.

For older nestlings, the positive effects of temperature and food on growth are each supported in four of five of the path diagrams (Table 7.3). The effects of wind are again shown to be variable, while the seasonal effect on growth is supported by three of five diagrams which show a decrease in nestling growth later in the season.

Relationships Among Environmental Variables

The effects of temperature and wind on insect abundance are consistent in all diagrams, with wind having a strong negative effect and temperature a strong positive effect on insect abundance (Figure 7.4, Table 7.3). There is a weak trend towards a decrease in food availability later in the season, but this is not consistent or strong.

Possible problems in interpreting relationships among environment variables arise because dates are entered more than once into the growth path diagrams. The impact of this non-independence is addressed by analyzing the environmental data from day 25 - 55 for each year, with each date entered once. The path diagram for this data set is similar to those produced from the growth data sets. As in the growth path diagrams,

maximum temperature has a strong positive effect on insect abundance, and wind speed a negative effect (Figure 7.10). Both temperature and insect abundance also change with season, although the indirect effect of season on insect abundance, through the increase in temperature, is more important than the direct effect of season. Analyses of each year independently result in similar patterns, except that wind has no effect on insect abundance in 1990 and the direct effect of season on insect abundance varies in both magnitude and sign among years (Figure 7.11).

Effects of Rain

Rainfall occurred on relatively few days during the nestling period (Figure 7.2). The effect of rain on mass change was determined using ANCOVA with rain as a categorical variable and the continuous variables of hatch day and nestling age entered as covariates. When the criterion for including a day as a rain day is set at ≥ 25 mm rain, no effect of precipitation on growth is seen in either young or old nestlings (Tables 7.4 and 7.5). When this criterion is narrowed to include only days with ≥ 1 cm of rain, precipitation does emerge as a significant predictor of growth in both young and old nestlings (Tables 7.4 and 7.5). Using the same criteria in examining the effect of rain on the abundance of aerial insects shows no significant effect of rain on Log Bug Index (Table 7.6).

Environmental Effects on Feather Growth

Environmental conditions explain a small but significant proportion of the variation in growth of the ninth primary feather (Figure 7.12). Hatch day and the abundance of insects on nestling day 11 are

Table 7.3. Summary of environmental effects on nestling growth and aerial insect abundances from the hypothesis represented in the path diagram in Figure 7.1. Aerial insect abundances measured as Log Bug Index. Four data sets were analyzed for young nestlings: young 90 - 91, young 1992, day 1 -3 1993, day 3 -5 1993. Five data sets were analyzed for old nestlings: old 90 - 91, day 8 - 10 1992, day 10 - 12 1992, day 8 - 10 1993, day 10 - 12 1993. Effects of Log B. I. and Age on Insect Abundance were not tested.

		Growth		 Insect Abundance		
Young Nestlings	neg.	no effect	pos.	neg.	no effect	pos.
Hatch Day	1	2	1	2	1	1
Max. Temp.			4			4
Wind	2		2	4		
Log B. I.	2		2			
Age			2			
Old Nestlings	neg.	no effect	pos.	neg.	no effect	pos.
Hatch Day	3	1	1	2	3	
Max. Temp.	1		4			5
Wind	2	1	2	5		
Log B. I.	1		4			
Age	1					

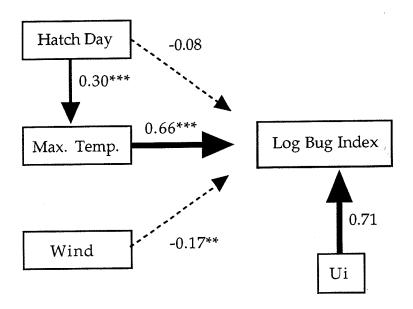


Figure 7.10. Path diagram of the relationships among environmental variables from 1990 -1993. Includes all available data from day 25 - day 55 in each year, with each date entered once. N = 111 days, $R^2 = 0.49$, p = 0.0001. See figure legend for Figure 7.4 for definitions and conventions.

Figure 7.11. Path diagrams of the relationships among environmental variables for each year. Includes all available data from day 25 - day 55 in 1990 - 1993, with each date entered once. For 1990, n=22 days, $R^2=0.45$, p=0.011. For 1991, n=31 days, $R^2=0.63$, p<0.001. For 1992, n=31 days, $R^2=0.69$, p<0.001. For 1993, n=27 days, $R^2=0.81$, p<0.001. See figure legend for Figure 7.4 for definitions and conventions.

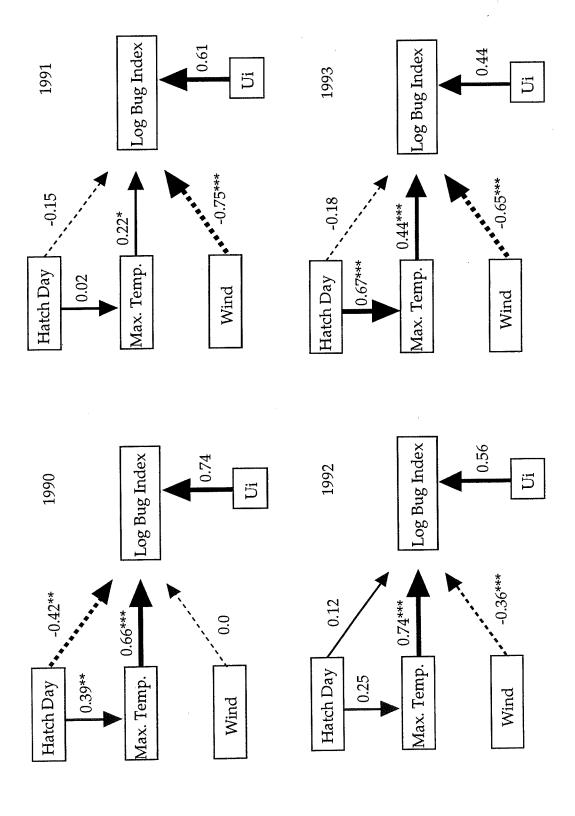


Table 7.4. Effect of precipitation on the growth of young nestling tree swallows. Rain is treated as a categorical variable in ANCOVA with age and hatch day controlled for. The criterion for including a date in the rain category is set at either ≥ 25 mm or ≥ 1 cm precipitation during the daylight hours. 22 of 131 broods met the criterion ≥ 25 mm rain, and 10 of 131 broods met the criterion of ≥ 1 cm rain.

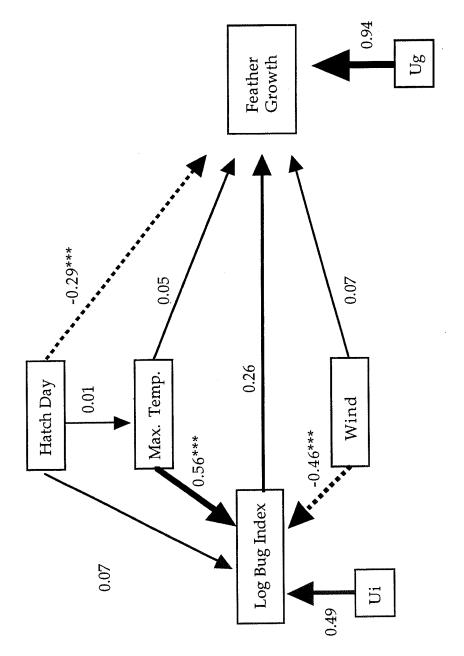
coefficient	standard. coefficient	<u>R</u> 2	F	p-value
-0.36	-0.12			0.12
-0.07	-0.35			< 0.001
0.77	0.39			< 0.001
		0.27	15.43	<0.001
coefficient	standard. coefficient	<u>R</u> 2	F	p-value
-0.92	-0.21			0.005
-0.07	-0.35			< 0.001
0.78	0.40			<0.001
		0.30	18.06	< 0.001
	-0.36 -0.07 0.77 coefficient -0.92 -0.07	coefficient -0.36	coefficient R² -0.36 -0.12 -0.07 -0.35 0.77 0.39 coefficient standard. coefficient -0.92 -0.21 -0.07 -0.35 0.78 0.40	coefficient R^2 F -0.36 -0.12 -0.07 -0.35 0.77 0.39 0.27 15.43 coefficient R^2 F -0.92 -0.21 -0.07 -0.35 0.78 0.40

Table 7.5. Effect of precipitation on the growth of old nestling tree swallows. Rain is treated as a categorical variable in ANCOVA with age and hatch day controlled for. The criterion for including a date in the rain category is set at either ≥ 25 mm or ≥ 1 cm precipitation during the daylight hours. 32 of 143 broods met the criterion ≥ 25 mm rain, and 11 of 143 broods met the criterion of ≥ 1 cm rain.

Rain ≥ 25 mm	coefficient	standard. coefficient	<u>R2</u>	F	p-value
Rain	0.02	0.01			0.95
Hatch day	-0.04	-0.17			0.04
Age	-1.08	-0.30			< 0.001
Overall			0.11	5.94	< 0.001
Rain ≥ 1 cm	coefficient	standard. coefficient	<u>R</u> 2	F	p-value
Rain	-1.28	-0.20			0.013
Hatch day	-0.04	-0.19			0.019
Age	-0.91	-0.25			0.002
Overall			0.15	8.34	<0.001

Table 7.6. Effect of precipitation on aerial insect abundance. Rain is treated as a categorical variable with the criterion for including a date in the rain category set at either ≥ 25 mm or ≥ 1 cm precipitation during the daylight hours. Results of Mann-Whitney U-tests. Includes all available data from days 25 - 55 in 1990 - 1993.

Rain ≥ 25 mm	n	mean (log mg/h)	stand. dev.	mean rank	U-value	p-value
Rain	19	0.56	0.56	47.5	712	0.21
No Rain	92	0.73	0.66	57.8		
			1			
Rain ≥ 1 cm	n	mean (log mg/h)	stand. dev.	mean <u>rank</u>	U-value	p-value
Rain	5	0.29	0.56	34.2	156	0.12
No Rain	106	0.72	0.64	57.0		



from 1992 and 1993. For feather growth $R^2 = 0.12$, p = 0.02 and for Log Bug Index R^2 Figure 7.12. Path analysis of environmental effects on growth of the ninth primary. = 0.76, p = 0.0001. See figure legend for Figure 7.4 for definitions and conventions. Feather growth measured between nestling days 10 and 12. Data from 97 broods

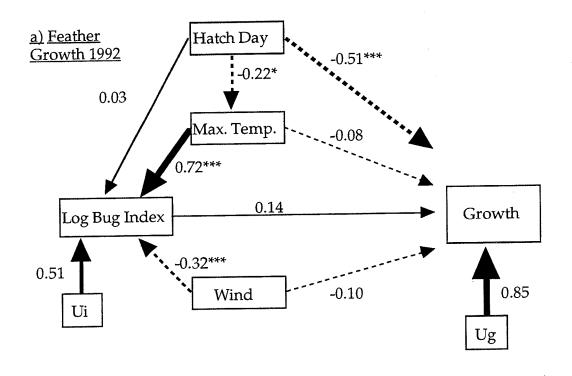
responsible for most of the variability explained, while temperature has a negligible direct effect. Each of the years examined separately show similar patterns, with the effect of the environment being more pronounced in 1992. Hatch day does not have a significant effect on feather growth in 1993 while a strong direct effect of wind does emerge in that year (Figure 7.13).

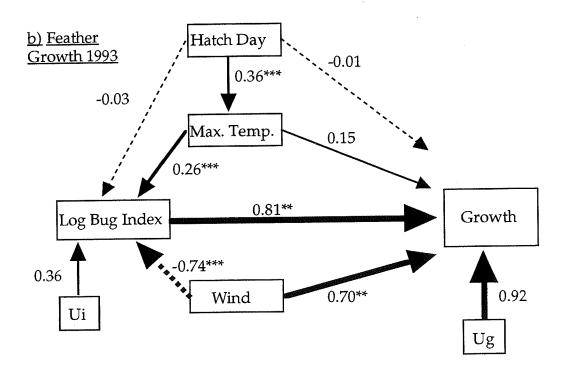
Since feather growth involves not only the accumulation of biomass, but the synthesis and differentiation of complex tissues, it is possible the effects of environmental conditions are delayed for one or more days after the exposure of the nestling. This was tested using the path diagram of the effect of insect abundance on the day of feather growth and the insect abundance on the preceding four days (nestling days 7 - 10). This analysis shows that environmental conditions several days prior to the day of feather growth can have significant effects on the growth of the ninth primary (Figure 7.14). Hatch day and the log of Bug Index for days 7 and 9 have the strongest direct effect on growth. Although insect abundance between adjacent days is correlated, the degree of correlation drops off quickly with more distant days (McCarty unpublished data).

Effects of Brood Size on Growth

Brood size for both young and old nestling age categories ranged from one to seven. Average brood size for young nestlings was 5.1 (stand. dev. = 0.9). Average brood size for old nestlings was 5.0 (st. dev. = 1.0). Brood size did not influence growth of either young or old nestlings (Figure 7.15). The prediction that brood size would become significant on

Figure 7.13. Path analysis of environmental effects on growth of the ninth primary. Feather growth measured between nestling days 10 and 12. Data from 1992 (Figure 7.13a) and 1993 (Figure 7.13b) were analyzed separately. In 1992, n = 40 broods, R^2 = 0.27, p = 0.02 for feather growth and R^2 = 0.74, p < 0.001 for Log Bug Index. In 1993, n = 57 broods, R^2 = 0.16, p = 0.05 for feather growth and R^2 = 0.87, p < 0.001 for Log Bug Index. See figure legend for Figure 7.4 for definitions and conventions.





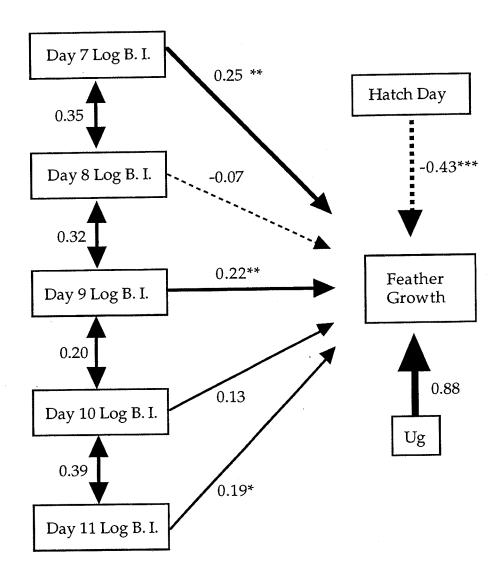
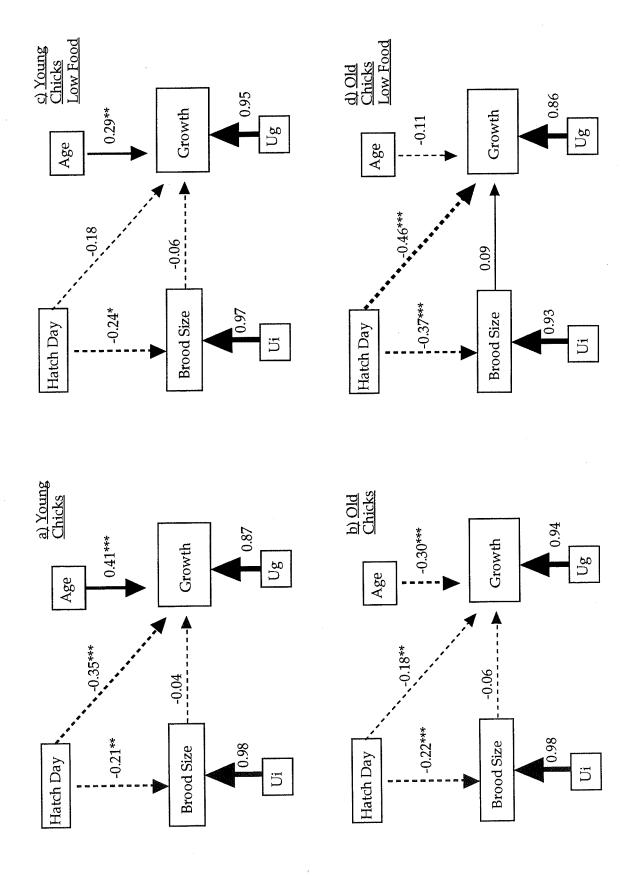
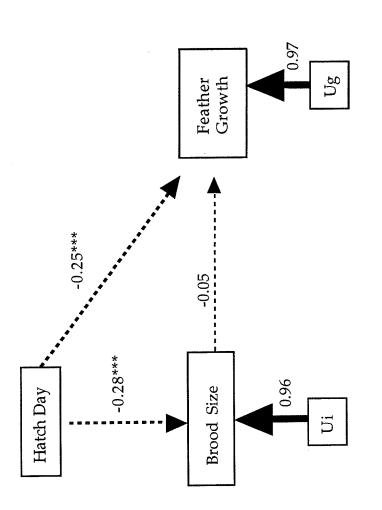


Figure 7.14. Relative importance of insect abundance on the days preceding measurement of feather growth. Feather growth is measured as the change in length of the ninth primary between nestling days 10 and 12. Insect abundance measured as the log of the Bug Index. Data from 97 broods. Overall $R^2 = 0.23$, p = 0.0006. See figure legend for Figure 7.4 for definitions and conventions.

Figure 7.15. Effect of brood size on growth of nestling tree swallows. Days with insect abundances greater than the median were excluded from Low Food paths (7.15c and d). The model for young nestlings (Figure 7.15a) includes 131 broods and has an $R^2 = 0.25$, p < 0.001 for growth and $R^2 = 0.04$, p = 0.019 for brood size. The model for old nestlings (Figure 7.15b) includes 143 broods and has an $R^2 = 0.12$, p = 0.002 for growth and $R^2 = 0.05$, p = 0.008 for brood size. Young nestlings from periods of low food abundance (Figure 7.15c) includes 74 broods and gives $R^2 = 0.10$, p = 0.074 for growth and $R^2 = 0.06$, p = 0.055 for brood size. Old nestlings from periods of low food abundance (Figure 7.15d) includes 70 broods and gives $R^2 = 0.26$, p < 0.001 for growth and $R^2 = 0.14$, p = 0.002 for brood size. See figure legend for Figure 7.4 for definitions and conventions.





between nestling days 10 and 12. Data from 97 broods from 1992 and 1993. For feather growth $R^2 = 0.06$, p = 0.049 and $R^2 = 0.08$, p = 0.001 for brood size. See figure legend for Figure 7.4 for definitions and conventions. Figure 7.16. Effect of brood size on the growth of the ninth primary

days with below average food was not supported (Figure 7.15). Brood size also had no effect on growth of the ninth primary between days 10 and 12 (Figure 7.16).

DISCUSSION

Environmental variation explains a substantial amount of the variability in nestling growth rates in tree swallows. Ambient temperature, as measured by maximum daily temperature, emerges as the best single indicator of this environmental variability, having both direct and indirect positive effects on growth. Given the importance generally given to food supply as a determinant of nestling growth, its relative unimportance for young nestlings may at first seem paradoxical. However, given the low energy requirements of young nestlings (see Chapter Four), it is not surprising that parents are capable of meeting the energy demands of such young birds under all but the most severe environmental conditions. Clark and Ricklefs (1988) formalized the importance of developmental stage in their model of parental care. The results presented in Figure 7.4 provide a test of one prediction of their model which states that:

"time allocation is constrained early during nestling development, primarily by the brooding requirements of small chicks, and later by food requirements of larger chicks." (Clark and Ricklefs 1988, p. 860)

My results are consistent with this prediction, with ambient temperature being an important determinant of growth for small nestlings, and food supply being important for old nestlings. The fact that ambient temperature is also important for older nestlings does not contradict the model, but may be an indication that thermoregulation by older nestlings carries a measurable cost.

A low importance of insect abundance would also be expected if my measure of food supply, Log Bug Index, were subject to a large degree of random error. Two pieces of evidence suggest that this is not the case. First, the 12 m Rothamsted Suction Trap used has been shown to accurately sample the food supply of foraging tree swallows and to give a good estimate of the abundance of insects over a wide area (see Appendix One for results and additional references). Second, the strong relationship between Log Bug Index and the other environmental variables (discussed below) also suggests that this measure of insect abundance is not plagued by high levels of random error.

Wind speed was predicted to have a direct, negative effect on growth. This prediction was not upheld, and the direct effect of wind was as likely to be positive as negative. Similarly, the negative effects of precipitation were not as strong as expected (Table 7.4), with a significant reduction occurring only on days with over 1 cm rain.

In other studies of aerial insectivores raising offspring, environmental conditions have been shown to have important impacts on reproductive activity. Wind velocity and ambient temperature were both significantly correlated with feeding rate in nesting chimney swifts (Chaetura pelagica; Zammuto et al 1981), while in purple martins (Progne subis) temperature was not correlated with activity during the nestling phase, but wind velocity did have a significant effect (Finlay 1976). Lack and Lack (1951) performed a multiple regression analysis of the environmental effects on growth of the swift (Apus apus). They found an

increase in growth with temperature and sunshine and a decrease with rain and wind, although temperature was only significant in one of two years (Lack and Lack 1951). In the only previous study of an aerial insectivore to actually measure food abundance, Bryant (1975, 1978) analyzed the effects of several environmental variables on nestling growth in house martins (*Delichon urbica*). Using multiple regression techniques, he found both food supply and temperature had significant effects on growth in mass and no significant environmental effects on wing length were detected. Bryant (1978) also found brood size to be negatively correlated with growth in the house martin. This is in contrast to the present study, which found no evidence that brood size influenced growth, suggesting either that food is not limiting during the nestling phase for tree swallows or that they may be adjusting clutch size (and hence brood size) to an individual optimum.

Daily feather growth was also influenced by environmental conditions, especially the abundance of food (Figure 7.12). The importance of environmental variables was much stronger in 1993, while a strong seasonal effect was evident in 1992. The importance of food supply for several days prior to feather growth (Figure 7.14) supports the hypothesis that feather growth is influenced by environmental effects prior to actual growth. The result that the effects of low food abundance are spread out over several days may have implications for the technique of ptilochronology, which assumes daily nutritional state is directly reflected in the daily growth of feathers and that "metabolic latency" is minimized (Grubb 1989, 1992; see Murphy and King 1991 and Murphy 1992 for criticisms of ptilochronology). These results do support the basic premise,

however, that the environment can influence growth of feathers and that food supply is a good predictor of short-term variation in feather growth.

The relationships between food supply and other environmental variables, especially wind speed and temperature, are strong and consistent. Temperature has a strong positive effect on insects as would be expected and as has been found in previous studies (Freeman 1945, Wellington 1945, Williams 1961, Taylor 1963, Bryant 1973, Isard et al. 1990, Pitcairn et al. 1990, Jönsson and Anderbrant 1993). Wind is also known from other studies to have a negative effect on numbers of aerial insects (Freeman 1945, Williams 1961, Bryant 1973, Schaefer et al. 1985, Pitcairn et al. 1990). The 12.2 m Rothamsted Suction trap used in this study is designed to be immune to the effects of wind on trap efficiency (Muirhead-Thomson 1991). However, the possibility that the strong negative relationship found between insect abundance and wind speed is partly due to the decreasing efficiency of the suction trap at high wind velocities is difficult to eliminate (Schaefer et al. 1985). Although correction factors for the effects of wind on suction traps do exist, they are based on the assumption that wind has no direct effect on insect abundance, so at present there is no way to partition out the two effects of wind on my measure of insect abundance. The effects of precipitation on insect abundance are variable. As in the present study, Jönsson and Anderbrant (1993) found that intermittent rain had little effect on insect abundance, while in Bryant's (1973) study insect abundance was correlated with duration of rain, but not the amount.

Path analysis is an effective means of evaluating the relative importance of different environmental effects on nestling growth. By

determining which components of environmental variability are most important, we can better understand the overall effect of the environment on growth and better predict the ultimate response to environmental variability. For tree swallows several predictions can be generated about the effects of environmental variability on reproductive strategies. For example, these results predict that to maximize nestling growth as environmental conditions deteriorate, parents with young nestlings should increase the amount of time devoted to brooding while parents with older chicks should increase foraging effort. These predictions, combined with alternative predictions generated using other observations, can be a valuable tool for guiding future research. For example, in the above scenario, the results in Chapter Six would make an alternative prediction that, if conditions were bad enough, parents should not brood young nestlings but should allow nestling body temperatures to drop. This difference can not only be tested in the field but also suggests that additional important variables include the duration of adverse conditions and the lower critical temperature of nestlings of different ages.

Quinney et al. (1986) considered food to be the most important environmental variable determining growth rates in their study of tree swallows. While my results generally support the assumption that food supply plays a role in determining growth rates, this study also emphasizes the need to take into account other environmental variables that can be equally important. The magnitude of the effects on both mass and wing length found by Quinney et al. also emphasizes the contrasting effects of chronic food shortages versus short-term food shortages. In their study, food supply at the two sites studied varied by a factor of four over the

entire month of June, resulting in a 12 % difference in mass between sites and 14 % difference in ninth primary length. In the present study, daily fluctuations in insect abundance of a similar magnitude result in a 19 % decrease in the mass gain of old nestlings and a 10 % decrease in the growth of the ninth primary, emphasizing both the sensitivity of short-term growth to short-term changes in the environment and the relative buffering of feather growth from variability on the scale of a single day.

The results reported here emphasize the difficulty in answering the question of whether food or other environmental factors are limiting for birds during the breeding season. The magnitude of the peaks in insect abundance (Figure 7.3) relative to the median level of insect availability clearly suggests that food is superabundant during the breeding season, at least on some days. Conversely, it is clear that food is limiting for this population, as evidenced by both the instances of growth reduction associated with the low points in insect abundance seen in Figure 7.3 and by the occasionally high levels of mortality due to starvation (see Chapters Five and Six). Defining the level of insect abundance that the individuals and the population are adjusted to is not a straightforward task. Integrating insect abundances over days or even the whole season is misleading if those periods are longer than the period of the fluctuations in resource availability. For example, mean insect abundances were higher in 1992 than they were in 1993, but reproduction failed in 1992 due to nestling starvation occurring over just a few days (see Chapter Six). The picture of the tree swallow population that emerges from this analysis is that food supply is generally limited; daily fluctuations in insect abundance produce measurable changes in the growth of old nestlings with high

energy demands, but food supply does become super-abundant for short periods (Holmes et al. 1986). At the same time, other environmental variables, especially temperature, also have important direct and indirect effects on growth rates.

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APPENDIX ONE:

Evaluation of Methods Used in the Study of Tree Swallow Foraging Ecology.

INTRODUCTION

Accurate measurement of the available food supply is a major difficulty for field studies of avian foraging (Hutto 1990) and a reliable assessment of the available resources is required before sound conclusions can be drawn. Although, compared to other birds, the prey resources of Hirundines are relatively easy to identify and sample accurately, few studies have documented the effectiveness of their techniques in describing diet and prey availability. This appendix evaluates several assumptions about the measurements of prey availability and resource use. First, I compare results of two techniques for obtaining samples of nestling tree swallow diets. Next, I examine the effectiveness of observations of nest visits as an indication of foraging intensity. Finally, I evaluate the reliability of using the single 12 m Rothamsted Insect Survey suction trap as an indication of the insects available to foraging swallows.

METHODS

Diet Sampling Techniques

Adult tree swallows collect a bolus of insects before returning to feed their nestlings. Samples of the nestling diet were obtained using two methods (Chapter Two). First, in each year of the study, adults were captured while feeding nestlings, and insects were removed directly from the parent's mouth. The nest was then inspected for food items that had

been dropped (Quinney and Ankney 1985, Blancher et al. 1987). In 1989 and 1990, additional diet samples were obtained using an artificial nestling puppet. For this technique, a blind was placed directly behind a nest, and an observer operated an artificial nestling puppet, competing with the live nestlings for the insect boluses brought by the adults. When the adults fed the artificial nestling, it was quickly withdrawn and the bolus removed. For a more detailed description of this technique, see McCarty and Winkler (1991). All insect samples were stored in 70% ethanol and analyzed as described in Chapter Two.

Foraging Activity

The daily cycle of foraging activity was investigated in 1993 using focal observations of nests containing nestlings 10 or 11 days old. Each nest was observed for between 4 and 8 periods of 30 minutes each. During observation periods the number of visits to the nest by the parents was recorded. Observations spanned the entire period of foraging activity, from approximately 0600 h to 2000 h.

The number of visits to the nest as a reliable measure of foraging activity was evaluated by video-taping the interior of nest-boxes while parents were foraging. Observations were distributed throughout the nestling period. A visit was scored as a confirmed feeding visit if the parent's bill was inserted in the mouth of a nestling. If the parent appeared to be feeding but the actual contact was blocked from view, the visit was classified as unknown, and if contact was not observed and the parent did not behave as if it were feeding, the visit was considered a non-feeding visit. Sex of the visiting parent was recorded when known.

Insect Sampling Technique

Much of the work presented here is based on samples from a single 12.2 m Rothamsted Aerial Insect Trap (Macaulay et al. 1988) located at Unit One. By sampling at 12 m, the Rothamsted trap avoids the effects of local emergence events and approximates the geometric mean of insect density with altitude, giving the best single estimate of overall insect density (Taylor and Palmer 1972). Although the reliability of the Rothamsted insect sampler is well documented (Taylor and Palmer 1972, Macaulay et al. 1988, Muirhead-Thomson 1991), I tested several characteristics of the insect sample that are important to the current study; the effects of altitude, temporal variability, and spatial variability.

h. Insect samples were examined under a dissecting microscope and identified to order, with the exception of Diptera, which were identified to sub-orders Nematocera and Brachycera. Small numbers of spiders (Aranae) were found in both the suction trap and diet samples; these have been included in the subsequent analyses in the Other Taxa category. Large numbers of thrips (Order Thysanoptera) occasionally occur in the suction trap samples, however due to the small size of thrips (usually < 0.5 mm) and the fact that they were never observed in swallow diets, all subsequent analyses exclude thrips. Insects were also sorted into size categories of 0-3, 3-5, 5-7, 7-9, 9-11, 11-13, and > 13 mm in length.

Insect abundances are known to change with altitude (Freeman 1945, Johnson 1957, Taylor 1974, Isard et al. 1990). During 1991 and 1992, I examined differences in the abundance and composition of the insect

fauna at 2 m and 12 m by comparing the catch of the 12 m Rothamsted trap to the catch of a 2 m tall Johnson and Taylor Aerial Insect Trap (9 inch model, Burkard Manufacturing Co. Ltd., Taylor 1962; Service 1973, 1977) located 27 m from the 12 m trap. These traps sample air at different rates so, in comparing the absolute abundance of insects between the two heights, a correction factor was applied to the catch from the 2 m trap, by multiplying the total catch by 4.77. This correction factor is based on the ratio of the rate of air sampling of the 12 m trap (45 m³/min; Macaulay et al. 1988) to the rate of air sampling of the 2 m trap (9.44 m³/min; Burkard Manufacturing Co. Ltd.).

Temporal variation in insect abundance was examined on three days during June 1993. The catch from the 12 m Rothamsted trap was segregated by removing the catch every 3 hours. On these days the trap was started at 0600 h, with the first sample taken at 0900, and the final sample taken at 2100h. The catch from each period was then plotted against time of day both as total number of insects, and as the percent of the highest hourly catch for that day.

I tested for the importance of spatial variability on insect abundance on several scales. In 1991 and 1992, I compared the insect faunas of the two study sites, Unit One and Unit Two, by comparing the catches from identical 2 m Johnson and Taylor Aerial Insect Traps located at each site. These two sites are located 2.5 km apart. In 1992, I obtained samples from five additional, 1.5 m tall, enclosed cone suction traps (Southwood 1978, Wilkinson 1992). These traps were placed in three different arrays, with inter-trap distances ranging from 1 to 300 m. Day-long samples were collected for seven days for each array. Two different trap arrays were used

at Unit One, and one array was used at Unit Two. The correlation coefficient for each pair of traps was calculated for each array. These correlation coefficients were then plotted against the distance between the trap pairs to test for effects of distance between traps on the similarity in daily insect catch. The correlations between the 1.5 m traps and the 12 m trap were also calculated and analyzed as above.

RESULTS

Diet Sampling Techniques

Samples of nestling diets obtained using the adult trap and artificial nestling did not differ in the distribution of insect sizes, but samples obtained using the adult trap method did contain a smaller proportion of Nematocera and a larger number of Hemiptera than samples obtained using the artificial nestling (Table A1.1). Samples obtained by trapping adults were larger in both the number of insects and the mass of the bolus, but neither of these differences was significant (Table A1.2). One of the largest differences between the two methods was the frequency with which Odonata occurred in the samples (Table A1.1). Samples containing Odonata contained few other insects and this difference might be responsible for the differences in load size observed in Table A1.2. Direct observations of the food brought to the nest were made in association with the artificial nestling samples in 1990. After a sample had been obtained, parents were allowed to feed nestlings undisturbed. During this period notes on the general composition of the food brought to nestlings were recorded, including the presence or absence of Odonates in the food bolus. For both Unit One and Unit Two, the percent of boluses containing

Table A1.1. Comparison between the composition of diet samples obtained by the trap method and by the artificial nestling method in 1989 and 1991. Values given are means of percents \pm 1 SE. N = 64 for the trap method and N = 55 for the artificial nestling method. p - values for student's t-tests. * = means significantly different with an adjustment for multiple comparisons.

Taxa	Trap	Art. Nest.	p - value
Diptera - Nematocera	13.2 ± 3.0	28.6 ± 5.0	0.010*
Diptera - Brachycera	22.6 ± 4.0	21.6 ± 3.7	0.848
Hemiptera	36.3 ± 4.8	7.3 ± 2.4	<0.001*
Odonata	14.1 ± 4.1	30.7 ± 5.9	0.020
Other Taxa	13.8 ± 3.5	11.8 ± 0.3	0.669
Size (mm)			
0-3	26.6 ± 3.8	16.4 ± 3.1	0.043
3-5	32.4 ± 3.9	34.1 ± 4.2	0.766
5-7	12.5 ± 2.8	14.7 ± 2.8	0.582
7-9	6.6 ± 2.4	3.2 ± 1.2	0.238
9 +	21.9 ± 4.7	31.5 ± 5.9	0.199

Table A1.2 Comparison of the size of food boluses sampled with the trap method versus the artificial nestling method in 1989 and 1990. N= number of samples, items = number of food items / bolus, mass = total mass of bolus in mg. Differences in the number of items per sample and in the mass of samples were not significant (t-test = 1.745 p = 0.083; t-test = 1.507, p = 0.135, for number of items and mass respectively).

Method	Mean Items	se <u>Items</u>	Mean <u>Mass</u>	se <u>Mass</u>	N
Trap.	18.3	2.8	25.1	2.9	64
Art. Nest.	11.8	2.4	19.4	2.2	55

Odonates are quite high, indicating that the artificial nestling method is not overestimating the importance of Odonates in the diet (Table A1.3). It is also interesting to note that the percent of boluses with Odonates is significantly greater at Unit Two than it is at Unit One (Table A1.3).

Foraging Activity

Focal observations were made on breeding pairs at 8 nests. Intensity of tree swallow foraging activity was variable, but showed no obvious pattern with time of day (Figure A1.1). Foraging rates were quite high, with a mean rate of 23 trips per hour, and a maximum of over 50 trips per hour (Figure A1.1a). Intensity of foraging was usually highest after 1000 h, but intensities of 60 to 80 % of peak activity were regularly observed before 0800 h (Figure A1.1b).

Behavior of visiting parents inside the nest-box was recorded on videotape at a total of five nests over 16 observation periods. Observation periods averaged 29 minutes (st. dev. = 10.4 minutes). The sex of the visiting parent could be identified at 4 of the 5 nests for a total of 10 observation periods. Nestling age at the time of observation ranged from day 4 to 20 (mean = day 12.6, st. dev. = 4.4).

A total of 132 nest visits were recorded during the observation periods, giving a mean visitation rate of 18.2 visits per hour (st. dev. = 7.8). Feeding was confirmed for 126 of these visits, and was probable for an additional 3 visits (Table A1.4). The remaining three visits when feeding did not occur were all recorded at the beginning of a single observation period. The parents at this nest were agitated by the presence of the video camera and in at least 2 of the 3 non-feeding visits they were carrying food

but left the nest without feeding. Later observations of this nest showed that the parents were feeding normally.

Males and females behaved similarly when visiting the nest (Table A1.4). Females were responsible for more of the non-feeding and probable feeding visits, but these involved only two individuals. Most individuals fed at 100 % of their visits, and considerably larger sample sizes would be necessary to detect any significant differences between sexes.

Insect Sampling

Insect abundances rose slowly through the day, beginning at dawn (Figure A1.2a). For each of the three days with multiple samples available, the peak in abundance occurred after 1200 h (Figure A1.2b). There was no noticeable peak in abundance associated with the times just after dawn or before dusk (Figure A1.2a).

Insect densities were significantly greater at 2 m than at 12 m in both 1991 and 1992. In 1991 the mean daily catch (corrected for volume of air sampled) was 916 insects/day (se = 129) at 2 m and 267 insects/day (se = 32) at 12 m (paired t-test = -6.025, p < 0.001). In 1992 the mean daily catch was 929 insects/day (se = 185) at 2 m and 319 insects/day (se = 95) at 12 m (paired t-test = -5.927, p < 0.001). Assuming each trap is 100% efficient, the absolute density of insects in 1991 was approximately 3.1×10^{-2} insects/m³ at 2 m and 0.9×10^{-2} insects/m³ at 12 m. In 1992, absolute insect densities were approximately 3.1×10^{-2} insects/m³ at 12 m.

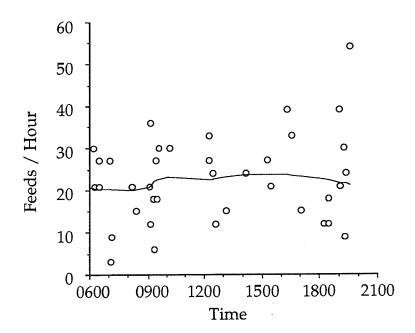
Table A1.3. Percent of boluses containing Odonates. Based on direct observations of food brought to nestlings during 1990. N = number of observation periods (each nest was observed for several observation periods, on separate days. Difference in percent of boluses containing Odonates between Unit One and Unit Two is significant (ANOVA F = 5.16, p = 0.028).

	Percent Odonates	se	N
Unit One	22.9 %	0.05	36
Unit Two	45.1 %	0.10	15

Table A1.4 Food delivery by parent swallows visiting nestlings. Observations from video recordings of five nests. Total visits includes all observations, male and female data include only those observations where the sex of the parents was known. n = number of observation periods. Visits Observed = all recorded visits, Feedings Observed = visits where feeding was confirmed, Probable Feedings = visits where feeding was likely but the feeding was blocked from view, Not Fed = visits where feeding did not occur.

	n	Visits Observed	Feedings Observed	Probable Feedings	Not Fed
Total Visits	16	132	126	3	3
Males	10	23	22	0	1
Females	10	45	41	2	2

Figure A1.1. Foraging intensity of tree swallows feeding young at different times of day. Based on 30 minute focal observations at 7 nests, each nest observed 4 to 8 times on one day. Figure A1.1a gives the rate of parents visiting the nest. Figure A1.1b gives the feeding intensity for each nest as the percent of the highest feeding rate for that nest. Smoothed LOWESS curves for each figure were fit using SYSTAT (Wilkinson et al. 1992)



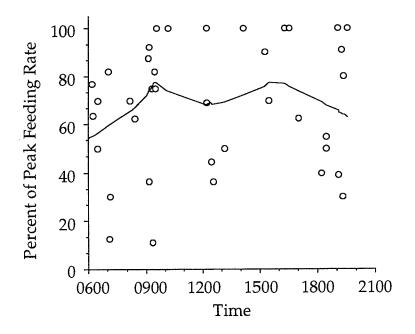
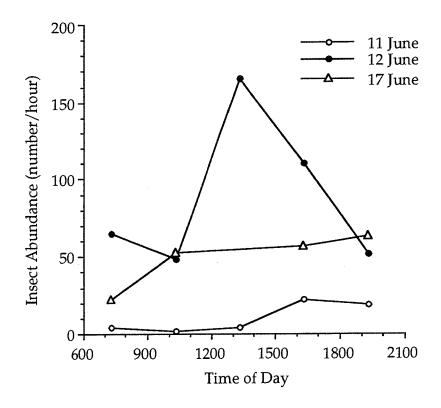
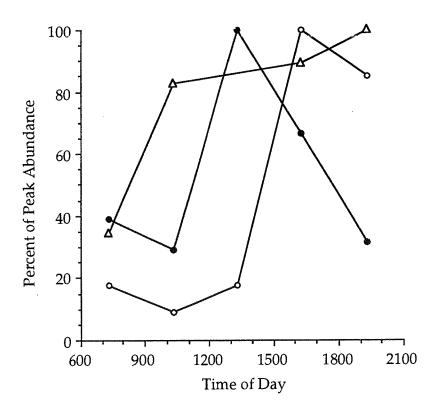


Figure A1.2. Change in the abundance of insects in the aerial plankton with time of day. Figures are based on samples taken every three hours during three days in June 1993. Lines connect data for each day. Figure A1.2a gives the average number of insects caught per hour. Figure A1.2b shows the percent of largest hourly catch for each time period for each day.





The size composition of the insect catches at two meters and twelve meters did not differ in either 1991 or 1992 (Tables A1.5 and A1.6). There were significant differences in the taxonomic composition between the two heights. Nematocera made up a larger proportion of the insect fauna at the lower altitude, while Hemiptera and other taxa were more frequent at the higher altitude (Tables A1.5 and A1.6).

The mean total daily catch of insects at 2 m was higher at Unit One in both 1991 and 1992. This difference was not significant in 1991 (paired t-test, p = 0.315), when the mean at Unit One was 192 insects/day (se = 27) and the mean at Unit Two was 147 insects/day (se = 35). In 1992 the mean catch at Unit One was significantly higher (paired t-test, p = 0.007), with a mean of 195 insects/day (se = 39) at Unit One, while the catch at Unit Two was 102 insects/day (se = 11). The distribution of insect sizes did not differ between the Ponds Units in either year (Tables A1.7 and A1.8). There were differences in the relative abundances of different orders, with Nematoccra being more prevalent at Unit Two and orders in the category Other Taxa being more prevalent at Unit One (Tables A1.7 and A1.8).

The correlation coefficients among the five 1.5 m traps were quite high, with a mean of 0.881 (n = 26, se = 0.018) for all pairwise comparisons. Further, when the correlation coefficients between two samplers are plotted against the distance between samplers, no effect of distance is found up to 300 meters (Figure A1.3), indicating that day-long samples are able to average out any spatial patchiness and that a single sampler will give a good indication of insect abundance available to birds. Correlations between the 1.5 m traps and the 12 m Rothamsted trap were slightly lower with a mean correlation coefficient of 0.630 (n = 14, se = 0.069). The

Table A1.5 Comparison of the percent composition of the aerial plankton at 2 meters and 12 meters at Unit One in 1991. Values given are means of percents \pm 1 SE. N = 47 for 2m and N = 48 for 12m. p - values for student's t-tests. * = means significantly different with an adjustment for multiple comparisons.

Taxa	2 m	12 m	p - value
Diptera - Nematocera	63.8 ± 2.9	45.4 ± 2.3	<0.001*
Diptera - Brachycera	6.2 ± 0.9	10.8 ± 2.0	0.043
Hemiptera	7.4 ± 0.8	17.2 ± 1.4	<0.001*
Other Taxa	22.6 ± 2.8	26.6 ± 1.6	0.204
Size (mm)			
0-3	92.2 ± 1.3	90.6 ± 1.6	0.443
3-5	4.1 ± 0.7	4.3 ± 0.6	0.848
5-7	1.9 ± 1.1	2.0 ± 0.4	0.946
7 +	1.8 ± 0.5	3.1 ± 1.5	0.430

Table A1.6. Comparison of the percent composition of the aerial plankton at 2 meters and 12 meters at Unit One in 1992. Values given are means of percents \pm 1 SE. N = 75 for 2m and N = 76 for 12m. p - values for student's t-tests. * = means significantly different with an adjustment for multiple comparisons.

Taxa	2 m	12 m	<u>p - value</u>
Diptera - Nematocera	78.8 ± 0.2	66.0 ± 1.9	<0.001*
Diptera - Brachycera	6.1 ± 1.3	6.0 ± 0.5	0.949
Hemiptera	4.7 ± 0.6	10.4 ± 1.2	<0.001*
Other Taxa	10.5 ± 1.5	17.6 ± 1.8	0.003*
Size (mm)			
0-3	92.1 ± 1.2	90.4 ± 1.2	0.339
3-5	6.5 ± 1.2	7.5 ± 1.1	0.534
5-7	0.6 ± 0.1	1.0 ± 0.2	0.166
7 +	0.8 ± 0.2	1.1 ± 0.4	0.571

Table A1.7. Comparison of the percent composition of the aerial plankton at 2 meters at Unit One and Unit Two in 1991. Values given are means of percents \pm 1 SE. N = 47 for Unit One and N = 46 for Unit Two. p - values for student's t-tests. * = means significantly different with an adjustment for multiple comparisons.

Taxa	Unit One	Unit Two	<u>p - value</u>
Diptera - Nematocera	63.8 ± 2.9	75.8 ± 2.4	0.002*
Diptera - Brachycera	6.2 ± 0.9	9.3 ± 2.0	0.172
Hemiptera	7.4 ± 0.8	5.3 ± 0.7	0.057
Other Taxa	22.6 ± 2.8	9.5 ± 1.2	<0.001*
Size (mm)			
0-3	92.2 ± 1.3	94.0 ± 0.9	0.243
3-5	4.1 ± 0.7	3.0 ± 0.6	0.241
5-7	1.9 ± 1.1	1.6 ± 0.4	0.767
7+	1.8 ± 0.5	1.5 ± 0.3	0.574

Table A1.8. Comparison of the percent composition of the aerial plankton at 2 meters at Unit One and Unit Two in 1992. Values given are means of percents \pm 1 SE. N = 76 for Unit One and N = 75 for Unit Two. P - values for student's t-tests. * = means significantly different with an adjustment for multiple comparisons.

Taxa	Unit One	Unit Two	p - value
Diptera - Nematocera	78.8 ± 0.2	85.6 ± 1.2	0.004*
Diptera - Brachycera	6.1 ± 1.3	4.4 ± 0.6	0.258
Hemiptera	4.7 ± 0.6	3.6 ± 0.6	0.221
Other Taxa	10.5 ± 1.5	6.3 ± 0.7	0.012*
Size (mm)			
0-3	92.1 ± 1.2	91.0 ± 0.8	0.501
3-5	6.5 ± 1.2	6.9 ± 0.7	0.788
5-7	0.6 ± 0.1	0.7 ± 0.1	0.941
7 +	0.8 ± 0.2	1.4 ± 0.4	0.206

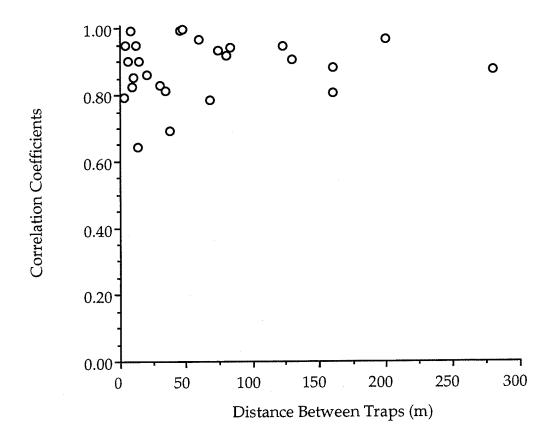


Figure A1.3. Correlation between weekly catches from pairs of 1.5 m tall suction traps versus the distance between each pair of traps.

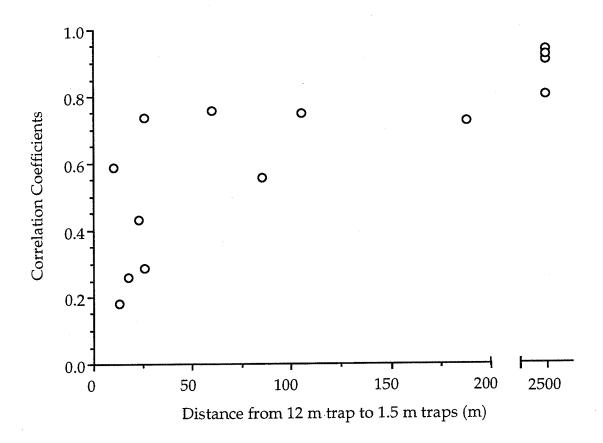


Figure A1.4. Correlation between weekly catches of five 1.5 m tall suction traps and the 12 m Rothamsted Trap, versus distance between the traps.

correlations between the 1.5 m traps and the 12 m Rothamsted trap were quite high during the week when the 1.5 m traps were located at Unit Two, 2.5 km from the 12 m trap with a mean correlation coefficient of 0.889 (n = 4, se = 0.031). The correlation coefficients showed a slight increase with distance from the 12 m trap (Figure A1.4).

DISCUSSION

The difficulty of obtaining an unbiased sample of prey items being used by birds is a chronic problem for studies of foraging ecology. Of the many methods available, those which obtain food items prior to ingestion will be most accurate (Blancher et al. 1987, McCarty and Winkler 1991). The two techniques used in this study, trapping adults and obtaining food boluses with an artificial nestling, obtain samples that are similar in size and taxonomic composition. The differences between the two techniques that do exist are not readily explained by characteristics of the methods themselves. Direct observations of food being delivered to nestlings suggests that the high proportion of Odonata recorded in the diet using the artificial nestling technique are a good approximation of the actual occurrence of these insects in the diet. The artificial nestling samples do consist of multiple diet samples from the same set of nests, raising the possibility of problems due to non-independence of samples from the same nest. Although the overall similarity of the results of the artificial nestling and adult trapping techniques support the assumption that differences among sampling days are more important than differences among nests, the difference in the importance of Odonates in the two types of samples

might represent an effect of multiple artificial nestling samples from a few parents specializing on Odonates.

Most samples of diet were collected between 0900 h and 1700 h. If tree swallows showed a peak in foraging activity at dawn or dusk, those samples might present a biased sample of resource use. The lack of a strong temporal pattern in foraging activity (Figure A1.1) suggests that samples obtained during mid-day are a good indication of overall feeding activity. Similarly, the lack of a sudden change in insect abundance between 1700 h and the cessation of tree swallow foraging activity (approx. 2030 h) indicates that the sampling period used (0630 - 1730 h) does not underestimate the abundances of insects in any systematic way. The results of the videotaping of nest-boxes confirm that visitation rate is a good approximation of feeding rate (Table A1.4).

Insect abundances may vary on a spatial scale smaller than the foraging range of tree swallows, in which case a single sample of available resources would not adequately characterize the prey available. In the vertical dimension, insect abundances do vary on a small scale, with abundance decreasing with altitude. Such a decrease in the abundance of aerial insects with altitude is well documented (Freeman 1945, Johnson 1957, Taylor 1974, Isard et al. 1990) and is unlikely to be solely an artifact of the different suction traps used at 2 m and 12 m. Although the change in absolute abundance is of ecological significance for tree swallows, the strong correlation between catches at 2 m and 12 m indicates that the single 12 m sample adequately describes temporal variation in insect density (Figure A1.4). The proportions of different taxa in the insect community also change with altitude (Tables A1.5 and A1.6). In both 1991 and 1992 the

relative numbers of Nematocera were higher at 2 m than 12 m and the relative numbers of Hemiptera were lower at 2 m than 12 m. Since both of these taxa consist of small, weakly flying insects, the differences between the samples are unlikely to be due to the lower suction velocity through the 2 m trap. A more likely explanation lies in the location of the traps near open water where Nematocera were emerging. The 12 m trap would obtain a sample integrating both this local emergence and insects carried from more distant sources likely to be the source of the Hemiptera captured.

Insect distributions also vary in the horizontal dimension. Although the 12 m Rothamsted trap is designed to be tall enough to be relatively immune to the effects of small-scale patchiness (Taylor and Palmer 1972), such variation has the potential to reduce the accuracy of single sample per day as a measure of available insects. The strength of the correlations between pairs of traps separated by up to 300 m (Figure A1.3) indicate that most effects of spatial variability in insect abundance were overwhelmed by the temporal variability found (Chapter Two, Figure 2.2). This seems to be true for distances as great as 2.5 km; the daily changes in insect abundance between the two Ponds Units were highly correlated, and their insect communities were generally similar (Figure A1.4, Tables A1.7 and A1.8).

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APPENDIX TWO: Growth and change in body compositions of nestling tree swallows.

The following tables provide detailed information on body measurements of nestling tree swallows of different ages. All of these measurements came from swallows breeding at the Cornell University Experimental Ponds Facility (42° 30' N; 76° 27' W), near Ithaca, New York between 1990 and 1993. Chapters Five and Six provide detailed methods on how these measurements were obtained.

Table A2.1. Masses and flattened, straightened wing chords of tree swallows of different ages. Mass measured to the nearest 0.1 g in 1990 through 1993. Adult mass from 1990 and fledgling mass from 1993. Measurements of flattened, straightened wing chord taken to the nearest 0.1 mm in 1990 through 1993.

Age	Mass (grams)	n, sd mass	Wing (mm)	n, sd wing
1	1.8	445, 0.3		_
2	2.6	184, 0.9	7.0	11, 0.9
3	3.8	661, 1.0	8.6	28, 1.2
4	5.4	308, 1.6	10.6	51, 1.6
5	7.6	580, 1.8	12.0	60, 1.7
6	10.1	187, 3.0	15.9	47, 2.5
7	12.5	474, 3.0	20.8	26, 3.9
8	15.2	515, 3.0	22.6	99, 5.1
9	17.1	647, 3.0	28.7	363, 5.2
10	19.1	700, 2.7	36.2	635, 5.9
11	20.4	129, 2.8	42.3	66, 5.5
12	21.2	638, 2.6	47.7	620, 6.1
13	21.2	60, 2.8	52.1	58,7.4
14	20.7	66, 1.8	56.3	54, 6.4
15	21.0	71, 2.6	62.0	72, 6.1
16	21.9	47, 1.4	64.8	47, 4.6
17	20.7	44, 1.7	73.1	40, 4.5
18	21.2	16, 1.3	74.9	16, 5.2
19	22.2	5, 1.9	79.6	5, 2.4
Fledge	19.9	3, 0.2	112.3	3, 1.5
Adult	21.3	187, 1.7	117.4	191, 3.6

Table A2.2. Manus and tarsus (i.e. tarsometatarsus) lengths of tree swallows of different ages. Measurements of manus derived from the difference between flattened, straightened wing chord and the length of the ninth primary measured to the nearest 0.1 mm in 1991. Adult and fledgling measurements of manus from 1993. Measurements of tarsus taken to the nearest 0.1 mm using dial calipers in 1990 and 1993.

Age	Manus (mm)	n, sd manus	Tarsus (mm)	n, sd tarsus
2	7.0	11, 0.9	5.1	11, 0.6
3	8.6	28, 1.2	6.7	33, 0.9
4	10.6	51, 1.6	7.4	47, 0.9
5	12.0	60, 1.7	8.5	60, 0.9
6	15.6	43, 2.2	9.8	53, 1.0
7	21.2	9, 1.6	10.9	22, 1.0
8	22.3	50, 2.3	11.7	41, 0.5
9	24.8	50, 1.5	12.1	13, 0.7
10	25.9	53, 1.2	12.3	41, 0.6
11	25.6	60, 2.1	12.2	25, 0.4
12	25.8	50, 1.9	12.0	6, 0.4
13	25.9	35, 2.2	•	
14	25.5	46, 2.2		
15	25.6	64, 3.5	12.1	12, 0.6
16	25.2	47, 1.5		
17	24.9	40, 2.1		
18	25.9	16, 3.9		
19	23.8	5, 0.9		
Fledge	24.3	4, 3.1	12.2	4, 0.9
Adult	24.9	10, 1.5	12.0	76, 0.4

Table A2.3. Length of flight feathers of tree swallows of different ages. Measurements of flattened, straightened feathers taken to the nearest 0.1 mm between 1990 and 1993.

Age	Ninth		First		Sixth	
-	Primary	y n, sd	Seconda	ry n,sd	Rectrix	<u>n, sd</u>
6	0.1	11, 0.3	0	4,0	0	4,0
7	2.0	15, 2.4	3.2	9, 1.6	1.5	13, 1.3
8	2.3	77, 1.8	3.8	33, 1.9	2.2	33, 1.4
9	4.2	359, 2.7	7.6	24, 3.7	5.1	24, 2.7
10	8.7	617, 4.3	10.1	35, 2.4	7.2	35, 1.9
11	16.3	60, 5.4	15.2	36, 5.4	9.8	36, 3.2
12	19.8	582, 5.8	20.0	34, 3.6	12.7	34, 3.3
13	27.0	35, 6.4	25.0	14, 6.0	16.8	14, 4.4
14	32.2	46, 4.5	29.5	5, 1.6	18.8	5, 0.9
15	36.2	72, 6.8	32.9	34, 4.7	21.4	27, 5.6
16	39.5	47, 5.2	38.7	4, 2.2	29.0	4,3.5
17	48.1	40,5.1	40.3	7, 1.9	29	7, 1.1
18	49.0	16, 8.6	41.9	5, 1.0		
19	55.8	5, 2.3				
Fledge	88.7	3, 2.9				
Adult	92.2	9, 2.9	49.1	8, 4.4	54.1	8, 2.3

Table A2.4. Pectoralis muscle mass of tree swallows of different ages. Means and (standard deviation) for nestlings collected in 1993. Age in days and all masses in grams.

age	wet mass	dry mass	% of total wet mass	% of total dry mass	% water	n
3	0.056 (0.015)	0.008 (0.002)	1.5 (0.3)	1.3 (0.3)	85.4 (1.6)	10
6	0.289 (0.095)	0.049 (0.017)	2.7 (0.1)	2.4 (0.1)	83.0 (0.6)	3
9	0.774 (0.182)	0.157 (0.036)	4.6 (0.9)	3.9 (0.6)	79.7 (1.2)	4
12	1.341 (0.378)	0.282 (0.083)	6.7 (1.3)	5.7 (1.2)	79.0 (0.8)	7
15	2.062 (0.219)	0.474 (0.059)	10.1 (1.1)	7.9 (0.9)	77.1 (0.6)	8
Fledge	2.053 (0.816)	0.622 (0.255)	13.3 (3.6)	11.6 (2.7)	70.0 (2.9)	4
Adult	2.652 (0.694)	0.820 (0.110)	16.0 (2.1)	13.4 (2.2)	67.4 (8.8)	6

Table A2.5. Body mass of tree swallows minus the pectoralis muscles and internal organs. Means and (standard deviation) for nestlings collected in 1993. Age in days and all masses in grams.

age	wet mass	dry mass	% of total wet mass	% of total dry mass	% water	n
3	2.584 (0.318)	0.400 (0.061)	70.3 (3.6)	64.6 (3.8)	84.5 (1.5)	10
6	7.415 (2.126)	1.354 (0.417)	68.7 (2.7)	65.1 (3.0)	81.8 (0.8)	3
9	12.021 (0.855)	2.801 (0.210)	71.2 (2.8)	70.8 (2.3)	76.7 (1.0)	4
12	13.428 (1.215)	3.401 (0.387)	68.2 (2.1)	69.0 (2.4)	74.7 (0.8)	7
15	13.431 (0.447)	4.161 (0.161)	65.7 (2.1)	69.6 (2.2)	69.0 (1.1)	8
Fledge	9.254 (1.567)	3.460 (0.924)	61.9 (2.7)	66.7 (3.3)	63.2 (4.7)	4
Adult	10.012 (2.083)	4.248 (0.723)	61.1 (4.1)	68.6 (3.2)	56.9 (6.3)	6

Table A2.6. Liver mass of tree swallows of different ages. Means and (standard deviation) for nestlings collected in 1993. Age in days and all masses in grams.

age	wet mass	dry mass	% of total wet mass	% of total dry mass	% water	n
3	0.226 (0.040)	0.047 (0.009)	6.3 (1.3)	7.6 (1.4)	79.3 (0.7)	8
6	0.905 (0.347)	0.207 (0.092)	8.2 (0.8)	9.7 (1.3)	77.4 (1.4)	3
9	1.193 (0.159)	0.295 (0.049)	7.0 (0.6)	7.4 (0.7)	75.3 (1.2)	4
12	1.515 (0.182)	0.386 (0.047)	7.7 (1.2)	7.9 (1.3)	74.5 (0.9)	7
15	1.394 (0.277)	0.370 (0.075)	6.8 (1.2)	6.2 (1.1)	73.5 (0.9)	8
Adult	0.711 (0.263)	0.231 (0.060)	4.4 (1.2)	3.8 (0.8)	65.9 (6.3)	5

Table A2.7. Mass of heart muscle of tree swallows of different ages. Means and (standard deviation) for nestlings collected in 1993. Age in days and all masses in grams.

age	wet mass	dry mass	% of total wet mass	% of total dry mass	% water	n
3	0.050 (0.012)	0.009 (0.003)	1.4 (0.3)	1.4 (0.4)	82.5 (1.3)	8
6	0.189 (0.044)	0.034 (0.006)	1.8 (0.5)	1.7 (0.4)	82.1 (1.2)	3
9	0.276 (0.075)	0.056 (0.010)	1.6 (0.4)	1.4 (0.2)	79.5 (2.2)	4
12	0.319 (0.072)	0.067 (0.013)	1.6 (0.4)	1.4 (0.3)	78.9 (1.2)	7
15	0.385 (0.130)	0.082 (0.023)	1.9 (0.7)	1.4 (0.4)	78.4 (1.3)	8
Adult	0.335 (0.091)	0.091 (0.019)	2.1 (0.3)	1.5 (0.2)	72.4 (3.4)	5

Table A2.8. Mass of the gastrointestinal tract of tree swallows of different ages. Means and (standard deviation) for nestlings collected in 1993. Age in days and all masses in grams.

age	wet mass	dry mass	% of total wet mass	% of total dry mass	% water	n
3	0.646 (0.103)	0.140 (0.019)	17.6 (1.8)	22.2 (2.1)	78.3 (1.6)	8
6	1.703 (0.585)	0.386 (0.137)	15.6 (1.0)	18.4 (0.8)	77.3 (1.2)	3
9	2.146 (0.250)	0.561 (0.074)	12.8 (1.7)	14.2 (1.6)	73.9 (1.7)	4
12	2.516 (0.236)	0.672 (0.082)	12.8 (1.0)	13.7 (1.2)	73.3 (1.3)	7
15	2.568 (0.358)	0.766 (0.151)	12.5 (1.6)	12.8 (2.0)	70.3 (2.3)	8
Adult	1.629 (0.551)	0.516 (0.176)	10.1 (2.3)	8.4 (2.2)	67.8 (5.4)	5

Table A2.9. Mass of the lungs, kidneys, and reproductive organs of tree swallows of different ages. Means and (standard deviation) for nestlings collected in 1993. Age in days and all masses in grams.

age	wet mass	dry mass	% of total wet mass	% of total dry mass	% water	n
3	0.060 (0.037)	0.010 (0.006)	1.6 (1.0)	1.7 (1.0)	82.5 (2.1)	8
6	0.339 (0.166)	0.059 (0.031)	3.0 (1.0)	2.8 (1.0)	82.8 (0.9)	3
9	0.461 (0.092)	0.089 (0.017)	2.8 (0.6)	2.3 (0.5)	80.6 (0.3)	4
12	0.580 (0.060)	0.117 (0.011)	3.0 (0.4)	2.4 (0.4)	79.7 (0.9)	7
15	0.621 (0.107)	0.130 (0.018)	3.0 (0.5)	2.2 (0.3)	79.0 (1.2)	8
Adult	1.068 (0.594)	0.276 (0.196)	6.6 (2.9)	4.4 (2.6)	75.1 (4.0)	5

Table A2.10. Mass of the internal organs of tree swallows of different ages. Means and (standard deviation) for nestlings collected in 1993. Age in days and all masses in grams.

age	wet dry % of total % of total mass mass wet mass dry mass				n	
3	1.039 (0.185)	0.211 (0.029)	28.2 (3.6)	34.2 (3.7)	79.6 (1.7)	10
6	3.137 (1.113)	0.687 (0.262)	28.6 (2.8)	32.5 (3.1)	78.2 (1.2)	3
9	4.076 (0.381)	1.001 (0.116)	24.2 (2.1)	25.3 (1.8)	75.5 (1.2)	4
12	4.929 (0.322)	1.242 (0.108)	25.1 (2.2)	25.4 (2.6)	74.8 (1.0)	7
15	4.967 (0.550)	1.347 (0.189)	24.3 (2.2)	22.5 (2.2)	72.9 (1.5)	8
Fledge	3.645 (0.364)	1.067 (0.091)	24.8 (4.6)	21.7 (5.5)	70.6 (2.6)	4
Adult	3.795 (1.052)	1.123 (0.316)	22.9 (3.6)	18.0 (3.5)	70.1 (3.6)	6

Table A2.11. Feather mass of tree swallows of different ages. Means and (standard deviation) for nestlings collected in 1993. Age in days and all masses in grams.

age	wet mass	dry mass	% of total wet mass	% of total dry mass	% water	n
3	0	0	0	0		10
6	0	0	0	0		3
9	0	0	0	0		4
12	0.959 (0.284)	0.384 (0.160)	4.5 (1.3)	7.3 (2.9)	60.6 (5.8)	5
15	1.191 (1.002)	0.914 (0.130)	8.2 (1.1)	13.1 (1.9)	52.1 (2.5)	5
Fledge	1.712 (0.374)	1.042 (0.107)	9.9 (1.5)	17.3 (2.8)	37.8 (8.7)	4
Adult	1.112 (0.887)	1.286 (0.100)	9.5 (1.7)	17.8 (2.0)	21.9 (8.4)	4

Table A2.12. Fat and water content of healthy tree swallows of different ages. Means and (standard deviation) presented for each age-class.

age	Lean-dry mass	Fat mass	% Fat	Fat Index	% water	Water Index	n
3	.415 (0.095)	0.082 (0.023)	2.9 (0.8)	0.20 (0.05)	80.3 (3.1)	5.66 (1.05)	12
6	1.771 (0.928)	0.419 (0.182)	4.4 (1.0)	0.25 (0.08)	77.4 (2.4)	4.41 (1.22)	5
9	2.870 (0.174)	0.923 (0.154)	6.6 (0.8)	0.32 (0.04)	71.7 (1.5)	3.50 (0.21)	4
12	4.331 (0.865)	1.168 (0.226)	7.1 (0.1)	0.28 (0.09)	69.8 (0.9)	2.71 (0.56)	7
15	4.923 (0.703)	1.884 (0.262)	11.2 (1.5)	0.39 (0.08)	64.6 (1.7)	2.26 (0.41)	8
Fledg	e 4.450 (1.520)	0.996 (0.722)	6.5 (4.0)	0.20 (0.12)	67.7 (5.3)	2.23 (0.68)	5
Adul	t 5.766 (0.441)	1.473 (0.747)	10.3 (3.7)	0.25 (0.13)	54.1 (8.5)	1.34 (0.48)	6

Table A2.13. Fat and water content of tree swallows that died during a period of inclement weather. See Chapter Six for description of age categories. Means and (standard deviation) presented for each age-class. Sample sizes given as number of nestling for fat calculation over (number of nestlings for water calculations).

age	Lean-dry mass	Fat mass	% Fat	Fat Index	% water	Water Index	n ·
3,	0.801	0.141	2.8	0.16	81.4	4.60	3
	(0.249)	(0.135)	(1.9)	(0.11)	(3.1)	(1.45)	(4)
6	0.968	0.175	3.3	0.18	81.1	5.78	4
	(0.307)	(0.076)	(0.3)	(0.07)	(0.2)	(0.03)	(2)
9	1.818	0.218	2.2	0.12	77.0	4.07	6
	(0.675)	(0.117)	(0.6)	(0.03)	(1.7)	(0.30)	(3)
12	2.261 (0.839)	0.239 (0.102)	2.0 (0.5)	0.11 (0.03)	77.9 (2.1)	4.08 (0.68)	11 (9)
15	2.820	0.263	2.0	0.09	75.6	3.63	13
	(0.351)	(0.069)	(0.3)	(0.02)	(3.2)	(0.60)	(11)
18	2.855	0.275	2.2	0.10	74.9	3.37	13
	(0.431)	(0.064)	(0.4)	(0.03)	(1.7)	(0.45)	(13)
20-30	2.950	0.261	2.2	0.09	71.5	2.83	19
Fledge	e (0.629)	(0.147)	(0.5)	(0.03)	(2.4)	(0.42)	(17)
Adult	5.711 (0.469)	1.043 (0.465)	8.4 (3.1)	0.18 (0.08)	52.7 (7.4)	1.14 (0.36)	4 (4)

Table A2.14. Dry mass of body components of tree swallows that died during a period of inclement weather. See Chapter Six for description of age categories. Means (number of nestlings, standard deviation) presented for each age-class.

age	Empty Body	Pectoralis	Liver	Heart	GI Tract	Other Organs	Pooled Organs
3	0.59	0.04 (1, 0)					0.21 (3, 0.10)
6	1.28 (4, 0.37)						
9	1.98	0.06	0.16	0.04	0.37	0.06	0.63
	(6, 0.92)	(2, 0.02)	(2, 0.03)	(2, 0.00)	(2, 0.04)	(2, 0.03)	(2, 0.01)
12	2.37	0.04	0.04	0.01	0.17	0.02	0.43
	(10, 0.95)	(3, 0.04)	(1, 0)	(1, 0)	(1, 0)	(1, 0)	(3, 0.17)
15	2.66	0.16	0.14	0.04	0.38	0.07	0.68
	(13, 0.62)	(9, 0.04)	(4, 0.02)	(4, 0.01)	(4, 0.08)	(4, 0.02)	(9, 0.14)
18	2.92 (13, 0.49)	0.24 (4, 0.04)					0.61 (3, 0.08)
20-30	0 2.96	0.31	0.10	0.05	0.26	0.05	0.43
Fled	ge(19, 0.58)	(5, 0.05)	(3, 0.03)	(3, 0.00)	(3, 0.02)	(3, 0.01)	(5, 0.05)
Adu	alt 3.81	0.72	0.22	0.10	0.41	0.36	1.11
	(4, 0.53)	(4, 0.20)	(3, 0.08)	(3, 0.01)	(3, 0.06)	(3, 0.37)	(4, 0.39)