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Patrick E. Lederle

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Ph.D. degree in Zoology

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**EFFECTS OF FEMALE AGE ON REPRODUCTION,
PARENTAL CARE AND GROWTH OF YOUNG IN TREE
SWALLOWS (*TACHYGINETA BICOLOR*)**

By

Patrick E. Lederle

A DISSERTATION

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ABSTRACT

EFFECTS OF FEMALE AGE ON REPRODUCTION, PARENTAL CARE AND GROWTH OF YOUNG IN TREE SWALLOWS (*TACHYCINETA BICOLOR*)

By

Patrick E. Lederle

It has been argued that clutch size in altricial birds is limited by the parent's abilities to adequately feed nestlings. In many species of birds, younger females breeding for the first time produce smaller clutches, and foraging deficiencies or inexperience have been thought to be the determining factors resulting in smaller clutches produced by younger females.

One-year old (SY) females initiated nesting later, laid smaller clutches, produced smaller eggs, and had a lower likelihood of hatching eggs, compared to older (ASY) females. I compared patterns of parental care and the resulting growth of young at four treatment groups characterized by age of female and brood size, to test the hypothesis that SY females are constrained from producing larger clutches by deficiencies in their abilities to care for young. Treatment groups were ASY nests with four young, ASY with six, SY with four and SY with six. During 1990, nestlings at SY nests with six young exhibited the poorest growth of any of the treatment groups

and this corresponded to the lowest rates of per young visitation rates by parents. Mortality rates were also highest for this treatment group. In contrast, during 1993, nestlings at ASY nests with six young received the lowest rate of per young visitation and growth measures were much more uniform between treatment groups. Results from 1990 appear to support the hypothesis that SY females may be constrained from producing larger clutches due to inadequate young rearing capabilities, yet the results from 1993 do not. During both years, comparison of parental visitation rates and measures of growth showed that within treatment groups, higher levels of visitation did not always translate into higher quality growth. This is likely due to differences in quality of parental care provided as opposed to visitation rates which only assess quantity. Analyses of growth variables and load sizes of food delivered to young which show significant effects due to the individual nest suggest that the performance of individual pairs of adults is more important in determining reproductive success than age of the female or brood size per se.

To Kate

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INTRODUCTION

Clutch size—the number of eggs laid by a female during one breeding attempt—is an easily measured variable of reproductive effort and determines the upper limit on reproductive output for a particular breeding attempt. David Lack, a pioneer in the development of clutch size theory in birds, hypothesized that the clutch size which evolved was the one that maximized the number of young which fledged (Lack 1947, 1954, 1966). He argued that the main factor in altricial birds which limited clutch size and the resulting number of fledged young, was the ability of the parent(s) to feed the young. Lack's hypothesis is appealing intuitively and has gained wide acceptance, this acceptance based mostly on brood enlargement studies that have shown that the most common clutch size is also the most productive in terms of producing young which fledge (*e.g.* Alatalo and Lundberg 1989, Crossner 1977, Lack 1954, Perrins 1965), yet few studies have been able to support his theory unequivocally (Bryant 1975, DeSteven 1980, Hussell 1972, Klomp 1970, Perrins and Moss 1975, von Haartman 1971). Some studies, in fact, have concluded that females are not optimizing clutch or brood size in relation to their abilities to feed young (Nur 1984, 1986). Nur showed that Blue Tits could successfully rear broods larger than the average clutch size (some much larger), and other studies have shown similar results (Bryant 1975, DeSteven 1980, Högstäd

1980, Loman 1980, Røskft 1985, Slagsvold 1982, among others). It is thought that larger clutch sizes which result in larger broods could have detrimental effects on both adults and their offspring. Adults attempting to keep up with the demands of artificially expanded broods have been shown to lose greater amounts of weight than those from control broods (Askenmo 1979, DeSteven 1980, Hussell 1972). Weight loss of adults during the feeding of young has been used as an indication that parents are stressed from the rigors of providing parental care (*e.g.* Hussell 1972, Nur 1984, Smith *et al.* 1988, yet see Freed 1981 or Norberg 1981 for alternative explanations), and young from enlarged broods often fledge at lower weights which can contribute to lower survival rates (Hochachka and Smith 1991, Magrath 1991, Perrins 1965, Smith *et al.* 1989).

Even though Lack's hypothesis has been both supported and refuted by various studies, it has provided ornithologists a powerful theoretical model from which to base years of productive research (Klomp 1970), and clutch size theory today is applied to many other taxonomic groups as well, such as invertebrates and even plants (Godfray, *et al.* 1991). Lack's hypothesis is easily understood when dealing with semelparous organisms where maximizing fitness for one breeding attempt (the only one in the individual's entire life) would be equivalent to lifetime fitness. The hypothesis becomes more difficult to apply in iteroparous organisms (those with repeated breeding attempts) where lifetime fitness is summed over all breeding attempts, and there are many factors, both intrinsic and extrinsic, which can limit or prevent breeding opportunities.

Because of this, Lack's hypothesis has been modified over the years, mainly due to the recognition that there are factors related to clutch size which can affect the fitness of young following fledging, as well as potentially affecting future breeding opportunities of adults. It has become more appropriate, yet many times not possible, to use a closer approximation of parental fitness than the number of young fledging, such as the number of offspring that survive to breed or the number of grandoffspring produced.

The Effects of Female Age on Breeding Performance

Females breeding for the first time have been observed in many species of vertebrates to produce smaller clutch sizes, and differ in other aspects of reproductive biology as well, when compared to older individuals (Clutton-Brock 1984, Salthe 1969, Tinkle and Ballinger 1972). This relationship has been observed most notably in birds (reviewed by Sæther 1990). In general, younger individuals or first-time breeders initiate nesting later, lay smaller clutches, produce smaller eggs, show a lower likelihood of hatching and fledging success, and produce fewer fledglings (DeSteven 1978, Finney and Cooke 1978, Hannon and Smith 1984, Harvey *et al.* 1979, Middleton 1979, Perrins and Moss 1974, Ross 1980, Sæther 1990, Stutchbury and Robertson 1988). There is also evidence that young which fledge from younger females breeding for the first time are of a smaller average size (Crawford 1977) and may be less likely to survive to breed (Lessells and Krebs 1989). The significance of the relationship between age and clutch size is underscored by Finney and Cooke (1978) who have

shown that although young female Snow Geese are less productive than older females, it is almost entirely due to initial differences in clutch size. Although clutch size differences between age classes of females are quite common, these differences are not universal (*e.g.* Bédard and LaPointe 1985, Erikstad *et al.* 1985, Hannon and Smith 1984, Leinonen 1973).

Two of the hypotheses explaining the differences in clutch size between first-time breeders and older individuals are the so-called *restraint* and *constraint* hypotheses (Curio 1983, Desrochers 1992). The restraint hypothesis argues that it is adaptive for first-time breeders to limit their reproductive output, whereas the constraint hypothesis assumes that younger breeders are deficient in some aspects of their abilities to produce offspring. These two hypotheses are not mutually exclusive (Curio 1983, Desrochers 1992, Wooller *et al.* 1990).

The restraint hypothesis predicts that natural selection would favor decreased reproductive output in younger, first-time breeders if it increased the probability of breeding again when they were older and more experienced (Charnov and Krebs 1974, Curio 1983, Stearns 1976, Williams 1966). At that time they would presumably be more likely to raise a larger brood due to increased age and experience (Finney and Cooke 1978, Hamann and Cooke 1987, Perrins and Moss 1974). Increased brood sizes have been shown to delay post-breeding molt (Slagsvold and Lifjeld 1989), delay breeding (Lessells 1986, Røskaft 1985) and decrease reproductive output in subsequent seasons (Gustafsson and Pärt 1990, Gustafsson and Sutherland 1988, Røskaft 1985), or

may lead to reduced adult survival (Askenmo 1979, Nur 1984, Reid 1987, yet see Alatalo and Lundberg 1989, or Alerstam and Högstedt 1984). Implicit in this argument is that older individuals would increase efforts to produce offspring as their reproductive value declined with age (Nol and Smith 1987, Reid 1988, Williams 1966) producing larger clutches and thus potentially fledging a greater number of young. Testing the restraint hypothesis requires a demonstration that a skill necessary for successful breeding is available to an individual yet is not utilized. The hypothesis is difficult to test because it is necessary to follow individuals through time and compare lifetime reproductive success of individuals that delayed breeding to individuals that bred at the first opportunity. Due to the problems involved with obtaining longitudinal data, particularly in short-lived species which migrate or do not show high site fidelity, complete data sets have been nearly impossible to obtain.

Testing the constraint hypothesis requires demonstrating that some of the skill or mechanisms necessary for successful breeding are lacking or deficient in younger breeders. The constraint hypothesis is supported circumstantially by many studies, many focusing on foraging abilities, which show that younger birds do less well than older individuals (reviews in Burger 1990, Marchetti and Price 1989, Wunderle 1991). It is postulated that younger birds breeding for the first time may be less able to provide food for themselves and produce smaller clutches as a result (Aldrich and Raveling 1983, Lack 1968, Perrins 1970, Perrins and Moss 1974). While some argue that deficiencies in providing parental care to the brood resulting from inadequate foraging

skills limit clutch size in younger birds (Ainley and Schlatter 1972, Bryant 1975, Jones 1987b and 1987c, Perrins and Moss 1974), others contend that limitations acting on the female during egg formation and incubation limit clutch size (Hussell and Quinney 1987, Nur 1984, Yom-Tov and Hilborn 1981). Food supplementation studies (Desrochers 1992, Källander 1974) have shown experimentally that young breeders start breeding earlier than normal when provisioned with additional food, and Desrochers (1992) demonstrated that it was because young females were less successful at finding food. Desrochers (1992) further concluded that although supplemental food did allow first-time breeders to increase the length of their breeding season compared to older individuals by allowing earlier nest initiation, they were still deficient in other aspects of reproductive performance as evidenced by lower annual reproductive output. In addition, there may be physiological or developmental constraints which contribute to observed differences in clutch sizes between age classes. Westin 1989 (cited in Enoksson 1993) showed that the ovaries and follicles of one-year old Willow Tits (*Parus montanus*) were smaller than those from older females, and smaller clutches and eggs potentially result from these size differences.

The mechanisms causing smaller clutch size and subsequent reduced reproductive output by females breeding for the first time are poorly understood. As Ricklefs (1977) points out, aspects of reproductive effort manifest themselves differently depending upon which of the many factors (*e.g.* age, territory quality, food supply, predation pressures) contribute to reproductive success or failure in any one breeding

attempt. Many potentially important yet subtle differences in behavior or physiology are difficult or impossible to measure in the context of field studies. As a result, most researchers have been able to measure only fecundity or mortality as a function of initial clutch size, and more subtle measures, often out of necessity, have been ignored.

Tree Swallows (*Tachycineta bicolor*) are unique among North American passerines because young adult females have a distinct subadult plumage (Rohwer *et al.* 1980) which makes it possible to assign females to age classes based on plumage characteristics (Hussell 1983a, USFWS and CWS 1991). Females in their second calendar year of life (SY—second year) can be distinguished from females that are older (ASY—after second year), and these characteristics represent an unusual opportunity to investigate questions concerning age-related reproductive performance. In many species of birds, female ages can be determined with confidence only if the individual was marked prior to fledging and then returned to breed in subsequent years.

It would seem that in a short-lived passerine, selection would favor early aged breeding, if at all possible. In Tree Swallows, which have an average expected lifespan of only 2.7 years (Butler 1988), each breeding season represents a significant portion of an individuals' potential reproductive output, so the benefits of early breeding are very high (Perrins and Moss 1974, Studd and Robertson 1985, Wittenberger 1979). In addition the effects of adult survival on average fitness will have less impact on short-lived species (many passerines) when compared to longer-lived species (such as many

seabirds), further suggesting that breeding by younger females would be favored if at all possible (Charnov and Krebs 1974).

Tree Swallow SY females have been shown generally to initiate nesting later, lay smaller clutches with lower egg weights, and produce smaller broods and fledge fewer young than ASY females (*e.g.* DeSteven 1978, Stutchbury and Robertson 1988). Previous studies on Tree Swallows have focused on relating observed differences in clutch size between SY and ASY females to nesting chronology, growth of young, fledging success and survival of adults (DeSteven 1978, 1980, Lombardo 1991, Stutchbury and Robertson 1988). The objective of this research was to investigate patterns and processes of reproduction and parental care in Tree Swallows as related to the age of the female parent in an attempt to clarify the mechanisms underlying the observation that SY females produce smaller clutch sizes. More specifically, this study attempts to answer the question of whether or not female Tree Swallows breeding for the first time are constrained from producing larger clutches by their abilities to provide parental care to the young they produce. This study is unique in that it attempts to test if the ability to provide parental care in Tree Swallows is an important factor in determining clutch size for this species. Because of the general observation of breeding deficiencies in first-time breeders (Sæther 1990) and, specifically, smaller clutch sizes in first-time breeders, coupled with Lack's postulated relationship between clutch size determination and parents' abilities to provide food for the young, the following working hypotheses and predictions were formulated:

1. Tree Swallow SY females have been shown to lay smaller clutches and produce lighter eggs than ASY females. If improvement is age-related, both clutch size and egg weights will increase when SY individuals breed again upon reaching the ASY age class.
2. Growth of young is influenced by the quantity and/or quality of parental care and those nests with the highest level of parental care will produce young with the best growth. Specifically, the growth of young at SY nests will be poorer, because parents at SY nests will provide lower levels of parental care.
3. Experimentally enlarged brood sizes will accentuate any deficiencies on the part of parents at SY nests by increasing the level of difficulty associated with rearing young. This will be reflected in poorer growth of young and smaller maximum size attained prior to fledging. In addition, parents at ASY nests will be better able to provide increased levels of parental care to larger broods.
4. The rigors of providing parental care are reflected in the condition of the parents as well as the young. Experimentally enlarged brood sizes will accentuate any potential deficiencies on the part of the parents at SY nests and this will be reflected in greater weight loss by parents at SY nests during the time of feeding young.

TREE SWALLOW NATURAL HISTORY

Tree Swallows are obligate secondary cavity-nesters which breed across much of North America. The southern limit of their breeding range extends across the central United States and the northern limit is the tree line. Populations are distributed based on the availability of nesting sites, and in some areas Tree Swallow populations are limited by the availability of artificial nestboxes (Austin and Low 1932, Chapman 1935, Holroyd 1975, Kuerzi 1941, Low 1933).

Tree Swallows are aerial insectivores, yet sometimes consume plant material, especially berries, fruits and seeds during periods of poor weather when insects are unavailable (Chapman 1955, Turner and Rose 1989). Adults generally feed on medium sized insects (4-6 mm long) and prey items taken closely correspond to insects which are available within one or two km of the nesting area (Kuerzi 1941, Quinney and Ankney 1985). As such, the diet varies by location, and site specific insect abundance has been shown to influence clutch size (Hussell and Quinney 1987).

Migrants arrive at breeding sites approximately one month prior to nest building. Adults have been shown to return to the same general breeding area as previous years, with reports of adults using the same nest cavity as previous years (Turner and

Rose 1989, personal observation). There are also anecdotal reports of females being less likely to return to the same area to nest if they have been unsuccessful (Cohen 1981, Turner and Rose 1989). Juveniles, whose return rates are generally very low, are reported to return to their natal area to breed (Butler 1988, Houston and Houston 1987). Adults are not territorial in the classic sense, yet defend an area of approximately 15 m radius around the nest (Robertson and Gibbs 1982) by chasing intruders and excluding others from the nest by perching in the entrance hole. The female collects most of the material for the nest which she builds over the course of several days to two weeks. The male collects feathers for lining the nest, and feathers have been demonstrated to provide a positive influence on the growth of young by providing additional insulation (Winkler 1992).

There are reports of populations of non-breeding Tree Swallows (termed “floaters”) which do not breed because of severe competition for nesting sites. It has been estimated in a well studied Ontario population that approximately 25 % of all females were floaters, and 50-80 % of these floaters were members of the SY female age class (Stutchbury and Robertson 1985, 1987a). The unique and distinguishable plumage of SY females has been hypothesized to suppress aggression from pairs established at nest sites by signaling to the resident female that the intruder is a subordinate and at the same time signaling to the resident male that the intruder is a female (Stutchbury and Robertson 1987b).

Females are monogamous and single brooded, although there have been cases of polygyny reported in very high prey abundance areas (*e.g.* Quinney 1983) and there have also been a few reports of two broods being produced in one season (Hussell 1983b). Eggs are laid generally at daily intervals, yet sometimes days are skipped, particularly during poor weather. Incubation lasts for approximately 14 days and only the female sits on the eggs, although there have been anecdotal reports of males incubating (Kuerzi 1941). Incubation often begins with the laying of the penultimate egg, and this leads to asynchronous hatching with the last egg hatching one day later than the rest of the clutch (Zach 1982). Brooding of the young is undertaken primarily by the female and effective thermoregulation of the brood in an enclosed nestbox occurs at approximately four days (Dunn 1979). Both females and males feed the young, bringing approximately equal amounts of food (Quinney 1986). Young fledge from the nest at approximately 18-21 days of age, depending upon the weather, and generally do not return to the nest following fledging (Turner and Rose 1989). There is little evidence that any post-fledging parental care occurs, yet Wheelwright *et al.* (1991) mention unpublished data showing that adults guard and feed young for several days following fledging.

Nesting success for Tree Swallows is highly variable from year to year due to the unpredictable insect food supply. Butler (1988) reports an average from several studies that 76% of eggs which are laid produce young which fledge. The population considered in this study showed a much lower success rate, with only approximately

45% of eggs laid resulting in fledged young over eight years (Beaver *et al.* 1994). Cold and wet weather can have a severe impact on fledging rates by causing mortality of young in the nest. Chapman (1955) reported mortality rates of young ranging from 6-44%, while Beaver *et al.* (1994) report a 95% loss in one year, 75% in another and 55% in a third. All three of these years were characterized by prolonged episodes of cold and wet weather when insect food was virtually unavailable (personal observation).

Following the breeding season, flocks congregate near bodies of open water and then migrate to the southern United States, Central America and the Caribbean. Sometimes the rare individual moves as far south as the western coast of Argentina. Adults undergo a complete molt following breeding from approximately mid-July through October. This time period of molt sometimes conflicts with late breeders still feeding young (Hussell 1983b), as well as coinciding with the migration period (Stutchbury and Rohwer 1990).

Although individual Tree Swallows have been known to live for up to eleven years (Hussell 1982), on average they live for only 2.7 years (Butler 1988) which is typical for small passerines (Bulmer and Perrins 1973). Mortality rates are about 60% for adults and may be higher for SY adults (Butler 1988, Houston and Houston 1987, Lombardo 1986).

METHODS

Study Sites

This study was conducted during 1989-1994 on state-owned land at Panola Plains (T42N R32W, Section 10), seven miles south of Crystal Falls, in the Upper Peninsula of Michigan. Additional data were collected during 1993 at Tachycineta Meadows (T42N R31W, Section 3), 12 miles east of Crystal Falls. Some additional clutch size and fecundity data from Panola Plains collected prior to 1989 are included for comparison. Both study areas were located in large openings which had been maintained by the Michigan Department of Natural Resources using fire and herbicide treatments during the 1960s and 70s in an attempt to provide habitat for Sharp-tailed Grouse. Each area has had resident populations of Tree Swallows since 1984 when grids of nestboxes were deployed in order to establish the areas as control plots for studies on potential effects of electromagnetic fields from the Navy's Project ELF (see Beaver *et al.* 1994). Panola Plains is situated on a glacial outwash plain with soils dominated by loamy sands (Vilas-Karlin complex, USDA Soil Conservation Service 1992). Predominant vegetative cover consists of low woody shrubs: specifically, sweet-fern (*Comptonia peregrina*) and blueberry (*Vaccinium* spp.), interspersed with areas of bracken (*Pteridium aquilinum*), and various species of grasses, forbs and sedges. Aspen

clones (*Populus tremuloides*) and scattered groups of *Amelanchier* spp., *Salix* spp., *Crataegus* spp. and *Prunus virginiana* which have grown up since cessation of burning and other habitat management treatments in the late 1970s, were interspersed with the nestboxes. Tachycineta Meadows is also situated on a glacial outwash plain of very fine sandy loam soils (Oconto series, USDA Soil Conservation Service 1992), yet the predominant vegetative cover is very uniform and consists of several species of grass, with only very sparsely distributed clumps of *Salix* spp. and *Amelanchier* spp. and a few scattered jack pines (*Pinus banksiana*). The small aspen clones which were present on the site when the initial nestboxes were deployed, were removed by roller-chopping in 1987 by the Michigan Department of Natural Resources, Wildlife Division. Nestboxes constructed of rough-sawn white cedar (9.4 cm W × 15 cm D × 22.5 cm H, inside dimensions), were placed on cedar posts approximately 1.5 m high and the posts were wrapped with high-density polyethylene to discourage climbing predators (Lederle *et al.* 1985). The front panel on the boxes was latched and hinged to allow easy access to the nest contents. Nestboxes were placed approximately 30 m from their nearest neighbor. This spacing has been found to be a preferred inter-nest distance for this obligate hole-nesting species (Muldal *et al.* 1985, Robertson and Rendell 1990). Originally, there were 75 nestboxes at Panola Plains and this number was increased to 100 in 1988, 125 in 1989, and 165 in 1990 and for the remainder of the study. Tachycineta Meadows originally had 75 boxes and this number was increased to 100 for the 1993 field

season. Tree Swallow occupancy rates on both sites have averaged greater than 80% since 1987.

Egg Weights and Hatching Times

Nestboxes were checked daily during the nesting period in order to assess any nesting activity which occurred. From these daily checks, generally made between 0630 and 1200 CDT, basic measures of reproductive activity were recorded: date of first egg laid, subsequent egg laying, total numbers of eggs laid (clutch size), numbers of eggs hatching, numbers of young fledging, and any mortality of young. Eggs at Panola Plains during 1990-1994 were marked lightly with a sequence number using a pencil on the first day they were observed, and weighed with a 5 g capacity Pesola® spring scale readable to the nearest 0.05 g. Weights were taken with the spring scale hanging inside a specially designed weighing box which ameliorated the effects of wind and rain on measurements. Spring scales were calibrated periodically (every 2 or 3 days, more frequently in wet weather) using a set of standard weights (Fisher Scientific) through the full range of the scale, with particular attention paid to the range of weights represented by the eggs being weighed. Occasionally an egg was missed on the first day it was laid due simply to not observing it in the nest or other logistical problems, so these eggs were weighed on the day following laying. First and second laid eggs were easily distinguished from one another by the size of the air space located in the blunt end of the egg; the first laid egg had the larger air space (personal observa-

tion). Eggs lose weight over time and Wiggins (1990) adjusted weights of Tree Swallow eggs missed on the first day by adding 0.02 g to the measurement on day two. I did not make this adjustment since the precision of the spring scales (measurement was possible to the nearest 0.05 g) used in this study was of a greater increment than the correction made by Wiggins.

During 1990-1993 egg weights were obtained by myself. During 1994 most of the weights were collected by a field assistant. In order to test for observer bias, 40 eggs from Tachycineta Meadows were weighed by both myself and the field assistant. Results showed that we measured weights slightly differently, yet, overall, these differences averaged only 0.008 g/egg less for the field assistant (less than 1/2 of 1 % of the mean). A one-way analysis of variance detected no differences between observers ($F = 0.039$, $P = 0.844$) and the observer factor explained far less than 1 % of the variability in egg weight ($R^2 = 0.001$). As such, no corrections were made for the 1994 egg weight data.

When nests neared the end of incubation and hatching was imminent (13-15 days after the last egg was laid), nests were visited more frequently (four times daily in 1989, three times daily 1990-1993, twice daily at Tachycineta Meadows in 1993) in order to establish hatching times. The first time a young was observed following hatching, it was marked by nail clipping and weighed with a Pesola® spring scale to the nearest 0.1 g. In addition, the condition of down was noted: wet or dry, matted or fluffy (Quinney *et al.* 1986). These distinctions allowed estimation of hatching times to

within two hours. Because eggs were numbered and nests were checked frequently, the egg from which a specific young hatched could be determined approximately 15-50% of the time.

Adult Weights and Measures

Adults were captured, generally while feeding young, using a simple nestbox trap (Magnusson 1984), or were handled in the course of daily box checks. Adults were banded using aluminum United States Fish and Wildlife Service bands if they were not already banded. Authorization for handling, color-marking and banding adults and young was secured from the proper state and federal agencies prior to the study through D.L. Beaver, Department of Zoology, Michigan State University (Master Permit #0966, my subpermit #0966-L). In addition, the Michigan State University Animal Care Committee approved the techniques and treatments used in this study, under the auspices of D.L. Beaver *et al.* (1994) ELF Project studies. Attempts were made each year to band as many adults as possible. As many young as possible were also banded, usually on day 16 following hatching. Adults were sexed by the presence of a distinct brood patch in females, or cloacal protuberance or lack of a brood patch in males. Females were aged using the criteria of Hussell (1983a). Females handled for the first time could most often be placed into one of two age categories by scoring the percentage of blue plumage on the dorsal surface of the body. The two categories (US Fish and Wildlife Service and Canadian Wildlife Service 1991) were: 1) SY, or *second*

year, which indicated that the female hatched during the previous calendar year breeding season and was actually approximately one year old, and 2) ASY, or *after second year*, which indicates that the female was at least two years old. These female age categories (SY and ASY) will be used throughout the remainder of the text. SY females were characterized by 0-50% coverage of dorsal blue plumage, and ASY females showed greater than 90% coverage. Females with 50-90% coverage are rare, yet are of uncertain age unless banded as nestlings, so were excluded from the study. Males do not show any plumage differences following their post-juvenile molt (Stutchbury and Rohwer 1990) and could only be aged positively if they were initially banded as young and then returned in later years. A minimum known age could be determined if a male was banded as an adult and returned in later years. Adults were handled once to determine age and sex and again only if necessary as part of the experimental treatment or design. Upon capture, adults were weighed to the nearest 0.1 g using a 50 g capacity Pesola® spring scale. Weights were taken by placing the adult head first into a coin envelope (#4, 11.5 × 7.5 cm) which held the bird without struggle and allowed easy release. The right wing chord was measured in a flattened position to the nearest mm using a stainless steel ruler fitted with a stop which allowed anchoring the wrist. During the 1990 field season I attempted to capture and weigh all treatment group adults (see below) a minimum of three times during the course of the nestling period in order to assess changes in body weight during the course of feeding young. Typically, weights were recorded on day 1 (day of hatching was day 0) or day 2 (rarely on days 0 or 3), on days 6, 7 or 8, and approximately day 14. There were many reasons why some

adults were not measured exactly on the day desired: weather, logistical problems, or difficulties with capture. Some adults were much easier (or more difficult) to capture than others. Although highly desirable, logistical problems prevented standardization of the time of day that adults were weighed. Wing chords were also remeasured upon recapture to assess repeatability within and across observers. Attempts were also made during 1991 to obtain multiple measures on all treatment group adults. I found that episodes of inclement weather caused adults to be in poor physical condition and the added invasiveness of capture was causing some nest abandonment, even though captures took place primarily during fine weather. Because of the problems in 1991, sequential adult weights and measures were not attempted during 1992-1994. Adults were color marked when necessary for behavioral study using "magic markers" (El Marko brand) for positive identification using video cameras or observing through binoculars. These colors faded after approximately seven days, so it was desirable to recapture treatment birds for remarking. This presented another opportunity for taking additional weights and measures, if desired.

Growth of Young

Young in the nest that had been originally marked by nail clipping which were included in the growth study were color banded (A.C. Hughes Ltd., Oxford, England) when they reached approximately 7 g. Growth of young at each of the nests under observation was assessed by visiting the nest every other day and taking measures of

weight to the nearest 0.1 g using a 10 g capacity Pesola® spring scale when the young were small and later a 50 g capacity spring scale also read to the nearest 0.1 g. Length of tarsus (tibiometatarsus), ulna, and wing (from elbow to tip of longest feather, or to tip of the fleshy part prior to feather eruption) were measured to the nearest 0.01 mm using a digital caliper (Multitoyo Digimatic). Data were entered on NEC PC8201A or PC8300 portable computers as they were collected in the field. Error trapping prevented entering of values out of the possible range of measurement. Young were only measured through day 16 (day of hatching was considered day 0) since nest disturbance after that time has been shown to increase the likelihood of premature fledging of young (DeSteven 1980, Kuerzi 1941, Paynter 1954, personal observation). Following day 16, nests were checked only briefly to determine if fledging had occurred, and during these checks the young were not handled unless absolutely necessary.

Parental Care Measures

Levels of parental care were quantified by observing the frequency of visits by adults to selected nests. The assumption was made that each visit constituted some aspect of parental care: brooding or feeding young, nest sanitation, nest defense or guarding, or more subtle behaviors. Nests were observed on days 1, 5, 9, 13 and 17 following hatching. These observation periods represent distinct phases of the nesting period. During day 1 most activity involved brooding of the young by females, sometimes for longer than 60 minutes. Although males visit just as frequently on day 1, the

duration of their visits is very short and probably does not involve brooding the young, since they are often observed perching with their head outside of the entrance hole.

Days 5, 9 and 13 represent a period of very rapid growth of the young and large numbers of visits/h generally occur on these days, particularly day 13. Maximum nestling weight has generally been reached by day 17, and the young often are entering a phase of weight recession at this time prior to fledging (Zach and Mayoh 1982).

During 1990, observations were conducted using video cameras. Once treatment nests were established on the day of hatching, video equipment (Canon VC200A cameras with Canon VR30A VHS format recorders or Canon E-61 8 mm camcorders) placed approximately 3 m from the nestbox entrance on a tripod, recorded visits to the nest by color-marked adults. A timer (Micronta model 63-5012 weather-resistant stopwatch) attached to the nestbox using velcro was used to indicate the time of day and allowed computation of the duration of each event. Observations were conducted at various times during the day depending upon weather, logistics and other observations scheduled on the same day. Nests observed with the VHS cameras were recorded for the duration of a 360 minute tape, those observed with an 8 mm camera were watched for the duration of a 120 minute tape whereupon the tape was changed and another 120 minute tape was recorded. An attempt was made to view each treatment nest alternately with each camera type throughout the study. In order to lessen the disturbance caused by setting up and taking down the camera equipment, a false camera setup was used on each treatment nest and remained in place from the day of hatching through fledging.

The only time the false setup was not in place was during actual observations. Each false setup mimicked the actual setup and consisted of a tripod constructed of 2 cm diameter electrical conduit painted in a camouflage pattern like the actual tripods used. A block of wood shaped like a camera was mounted atop the false tripod and was covered by a camouflage cloth bag of the same pattern used over the actual cameras. A small block of wood painted black served as a false clock and was attached to the nest-box using velcro. The adults adjusted to the presence of the equipment very rapidly, sometimes entering the box within five minutes after setup. During 1990, data on parental care were obtained by viewing the video tapes and recording information from each event on NEC PC8201A or PC8300 portable computers. Variables recorded for each event included: sex of parent making the visit, the duration of time spent in the nestbox, and whether or not a fecal sac was removed from the nest. The number of visits was standardized to a per hour basis to take into account differences in time under observation for each nest. Time under observation was computed for each tape as the time from the start of the first event recorded to the end of the last complete event on the tape.

During 1993, events were recorded manually by observing the focal nest with binoculars for a sampling time of one h during days 1, 5, 9, 13 and 17. This sampling technique allowed an increase in the number of nests observed from 16 in 1990 to 29 in 1993 (four in each treatment group in 1990 and a minimum of six in each group in 1993). In addition, because of the increase in the number of nests observed and the use

of two plots in 1993 in an attempt to increase sample size, it was not possible to use the video recording technique. Nests were observed with 8.5× or 10× binoculars from a distance of 50-150 m. The distance to the nestbox differed for each nest under observation due to terrain, distance to adjacent boxes (which was maximized) and availability of cover in which to locate the observation post. When setting up for observation, care was taken to note any alarm calls given by adults and the observation post was moved if alarm calls from adjacent nests persisted. Binoculars were held in a tripod system which allowed the observer to sit comfortably in a lawn chair and look through the binoculars without moving. Observers used personal communicators (Maxon 49-SX) which allowed constant contact between all members of the research team on the plot. This allowed perfect coordination of observations and other research tasks being conducted on the plot and eliminated any possible interference. In addition, any questions which arose could be dealt with in an immediate fashion rather than waiting for a later time.

Observations in 1993 were of one h duration and the number of visits by each adult were recorded. Although fecal sac removals could often be observed and they were recorded, manual observations did not have the benefit of instant replay, so I could not be certain of fecal sac removals and these data were not included in any analyses.

Establishment of Treatment Nests

Four treatment groups were established for comparison: 1) ASY nests with four or, 2) six young, and 3) SY nests with four or, 4) six young. Female ages were determined during the course of daily box checks by viewing the adults as they exited the nestbox, by observing through binoculars or by direct handling if past day ten of incubation. Handling of adults during egg laying and early incubation was avoided since this can lead to abandonment of the nest (Burt and Tuttle 1983, Cohen 1985, Lombardo 1989, personal observation). An experienced observer could make the distinction between ASY and SY females most of the time, and final determinations were made during handling to color mark the adults prior to any observations. Several nests were dropped from the study at this point because the adults fell into the unknown age category (Hussell 1983a). Treatment nests were established on the day of hatching. Decisions as to which nests were to be included in the treatment groups were based on age of the female and date of hatching. Treatments were established as rapidly as possible, the limiting factor being the maximum number of nests which could be observed on any one day, or the total number of young which could be measured for growth by one observer on any one day. Establishment of treatments took five days in 1990 and eight days in 1993. Hatching times were determined by visiting the nests frequently (see above) and if necessary, the number of young in the nest was manipulated so all young hatched within approximately eight hours of one another. Manipulations took place on the day of hatching and were used if it was necessary to increase the number of young

in the nest, decrease the number of young in the nest, or to even out cases of hatching asynchrony which is a common occurrence in Tree Swallows (Clark and Wilson 1981, Zach 1982, personal observation). If it was necessary to move young into a treatment nest, care was taken to choose a nestling that was hatched at approximately the same time as the rest of the young in the treatment nest and to assure that the weights of the young were approximately the same. These precautions helped eliminate any weight hierarchies which could confound results (Zach 1982). Manipulations took place at approximately the same time that nests were checked for hatching, so the manipulations did not significantly increase the amount of disturbance which was already occurring. It does not appear that Tree Swallow adults can distinguish between their own and fostered young (Beaver *et al.* 1994), and it is well established that the major influence on growth is the nest (*i.e.* parental effect) in which the young are raised, rather than the nest of origin (Beaver *et al.* 1994, Pettifor *et al.* 1988, Quinney *et al.* 1986, Ricklefs and Peters 1981).

Weight of Food Delivered to Young

During 1989, 1990 and 1991 the weight of food delivered to the young at selected nests was determined using the "ligature method" (Johnson *et al.* 1980). This involved placing around the young's neck a "ligature" or "collar" which constricted the esophagus and prevented swallowing. Once fed by an adult, the food bolus could be removed from the mouth and esophagus with forceps and stored in 70% ethanol for

further analyses. Collars were made of paper coated wire commonly referred to as “twist ties”, and stayed on the young for a maximum bout time of 75 minutes. Generally, bouts were much shorter, as longer times often resulted in disgorged boluses which tended to collect nest debris which contaminated the sample and potentially biased final bolus weights. All young in the nest were collared during a bout. Collaring took place generally at 5-14 days posthatch.

During 1989, from 30 June to 23 July, young were collared at 15 nests varying from three to five young per nest. Nine nests had ASY females, and six nests had SY females. From these nests 244 boluses were collected, many of which were collected and weighed as a group associated with one bout. Because of this, means of groups were used ($n = 94$ groups). During 1990, from 26 June to 13 July, young were collared at 21 nests with three to five young per nest. Fourteen nests had ASY females, and seven nests had SY females. From these nests 239 boluses were collected, and because some were collected as groups, an n of 177 was used in the analyses. No attempt was made to differentiate boluses delivered by the male or female parent, so during 1989 and 1990 only nest types categorized by female age could be distinguished.

Protocols were much different during 1991 when boluses were collected from six nests (three ASY and three SY) between 30 June and 18 July. Five nests contained four young and one of the SY nests contained only three young. Adults were captured prior to any bolus collection bouts and color marked for positive identification. When young were between one and four days posthatch, nestboxes were modified to open

additionally from the back and a blind was attached to the back of the nestbox. Blinds were constructed of lightweight wooden frames covered with cardboard sheets painted in a camouflage pattern. Each blind consisted of four panels screwed together making up the four sides and a similarly constructed roof. During deployment, modification of the nestbox, and assembling and attaching the blind to the nestbox took approximately 20 minutes. Tree Swallow adults readily accepted the blinds, some returning to feed young almost immediately after deployment was complete. Because the blind was attached to the nestbox, an observer inside the blind could open the nestbox and quickly remove boluses from young after an adult had left the nest. One observer was located in the blind to collect boluses, another observer was situated 75-150 m away from the nestbox hidden in vegetation, and it was this observer who determined the sex of the adult entering or leaving the nestbox based on color markings. Communication between observers was achieved using the radios described earlier. In this way it could be determined with confidence from which adult the food delivered had come from. Sixty-nine female and 43 male boluses were collected. The sex of the delivering adult could not be determined with confidence for an additional 24 boluses.

Samples were removed from ethanol and placed on pre-dried and pre-weighed filter paper (1989) or polystyrene weighing dishes (1990 and 1991). Samples were dried to a constant weight in an drying cabinet with the temperature maintained at 40°C for a minimum of 48 h (N. Walker, Dept. of Entomology, Michigan State University, personal communication). Dried samples (bolus plus weighing dish) were weighed to

the nearest 0.0001g using a Sartorius H51 or Sartorius 1207 MP2 electronic scale, and the final dried weight of the bolus was determined by subtraction.

Ambient Monitoring

Ambient temperatures were recorded at 9 minute intervals at both Panola Plains and Tachycineta Meadows beginning prior to egg laying and ending when all fledging had occurred on the plot. Temperatures were recorded using an On-site Weather Logger (O.W.L., EME Systems, Berkeley, CA) and an NEC PC8201A portable computer powered by a 12 v gel-cell battery. Data were collected by transferring files directly from the NEC to a portable disc drive (Purple Computer Products or Tandy). The temperature probes (microcircuit type, EME Systems, Berkeley, CA) were attached directly underneath a nestbox approximately 1.5 m above ground level insuring that they were situated in the shade at any time of the day (Christian and Tracey 1985). Prior to deployment, probes were calibrated using thermometers whose calibrations are traceable to the National Bureau of Standards. For this study, two temperature probes were used, one situated at a low elevation portion of the plot, the other at a high elevation portion of the plot. High and low elevations differed by approximately 5 m. Any temperature data presented is derived from an average of these two probes. Once appended to a database, data were scanned using error detection routines, corrected for probe calibrations, and hourly means were calculated.

Statistical Analyses

Prior to statistical analyses data sets were tested for normality using a combination of graphical and statistical techniques. Probability and stem/leaf plots were used to view the distribution of data, and statistical assessments for normality included the procedures outlined by D'Agostino *et al.* (1990) or Lilliefors' test (Lilliefors 1967). Variance heterogeneity was tested using either Bartlett's test or the $F_{\max}$ test. Bartlett's test is overly sensitive to departures from normality (Sokal and Rohlf 1981) so the $F_{\max}$ test was used in cases where this was a potential problem. If possible, data were transformed in an attempt to eliminate any problems with normality or variance heterogeneity. Means are presented with standard errors, and figures represent untransformed data unless otherwise noted. All statistical procedures were carried out using SYSTAT® (Wilkinson 1992). All tests were two-way unless otherwise noted as warranted by the type of hypothesis tested and $\alpha = 0.05$ was used as the standard to determine whether departures from the null hypothesis were significant. When using nested analysis of variance techniques, denominator mean squares used in the calculation of F ratios were determined using the methods outlined in Zar (1984, pp. 470-476). Other techniques are explained in the text where first used.

RESULTS

AGE-RELATED FECUNDITY

Percent SY Females In Population

The percentages of nesting SY females in the population under study at Panola Plains has ranged from 11.3% of the known age females in 1993 to 31.5% in 1994 (Table 1). These values are slightly lower when all of the females (including those of

Table 1. Percentage of breeding females in the SY and ASY age classes, 1987-1994.

Year	# ASY	# SY	# Unknown	Total Females	% SY Females	Total Known Age Females	% SY of Known Age Females
1994	74	34	21	129	26.4	108	31.5
1993	94	12	6	112	10.7	106	11.3
1992	94	24	10	128	18.8	118	20.3
1991	92	17	27	136	12.5	109	15.6
1990	95	23	12	130	17.7	118	19.5
1989	89	19	6	114	16.7	108	17.6
1988	49	14	16	79	17.7	63	22.2
1987	43	13	3	59	22.0	56	23.2

unknown age) in the population are included. Lombardo (1986) reported that 48.9% of all nesting attempts (laying at least one egg) were made by SY females, and that the proportion of SY's in the population remained stable from year-to-year. Stutchbury and Robertson (1985) reported that SY females accounted for 22.8% of breeding attempts. This value is likely inflated because SY females made up a high proportion of the floating population that was encouraged to nest by the provision of extra nestboxes later in the season. Interestingly, the lowest percentage of SY females in the Panola Plains population was recorded during 1993, following a geographically widespread weather-related mortality event during 1992. Mortality of nestlings was nearly 100% in nests at Panola Plains and surrounding populations of Tree Swallows (Beaver *et al.* 1994). Presumably, recruitment into the 1993 breeding population was low and resulted in small numbers of SY females. In contrast, the highest percentage of SY females breeding occurred during the following year in 1994. This may reflect increased breeding opportunities for SY females hatched in 1993 due to a potential decrease in ASY population levels associated with the lack of recruitment from the 1992 cohort.

Nest Initiation And Egg Laying

Egg laying started later, on average, for SY females during all years, except for 1987 (Figure 1). Data were corrected for yearly variation in nest initiation by counting from the day the first egg was observed for that year rather than counting from a fixed date (*i.e.* day 1 = day first egg was encountered in the population for that year). The

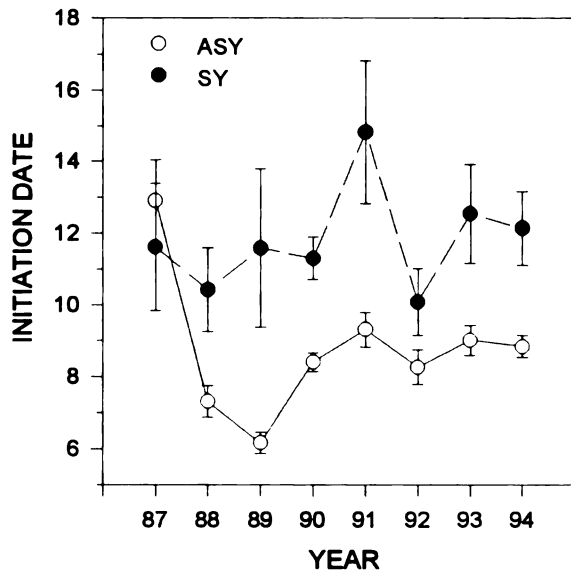


Figure 1. Mean nest initiation dates ($\pm$ S.E.) for SY and ASY females, 1987-1994.

distribution of laying dates was skewed toward low-numbered dates and could not be normalized by transformations, and variances were heterogeneous as well, so a Kruskal-Wallis one-way analysis of variance was used to compare the two female age groups. Computed on a yearly basis (Table 2), Kruskal-Wallis tests showed

significant differences between SY and ASY females in initiation dates for all years (all $P < 0.039$), except 1987. With data pooled across years there was a significant difference between the two age classes ($\chi^2 = 46.522$, $df = 1$, $P < 0.001$).

Although I could not meet all of the strict assumptions of the test, analysis of variance (Table 3) revealed a significant effect of female age on initiation date, with SY's beginning egg laying later in the season ($F = 51.150$, $P < 0.001$). Year-to-year fluctuations in the mean initiation dates (corrected for year) were also significant ($F = 4.725$, $P < 0.001$), and a significant female age $\times$ year interaction was detected ($F = 2.792$, $P = 0.007$) due to data from 1987 where the SY mean date was earlier than the ASY date (Figure 1).

Table 2. Comparisons of yearly nest initiation dates between SY and ASY nests using Kruskal-Wallis tests.

Year	Female Age	# Nests	Rank Sum	χ^2	P
1994	ASY	74	3605.5	8.132	0.004
	SY	34	2280.5		
1993	ASY	92	4549.5	6.361	0.012
	SY	11	806.5		
1992	ASY	94	5286.0	4.259	0.039
	SY	24	1735.0		
1991	ASY	91	4615.0	8.529	0.003
	SY	17	1271.0		
1990	ASY	94	4946.0	17.226	< 0.001
	SY	23	1957.0		
1989	ASY	86	4095.5	11.346	0.001
	SY	17	1260.5		
1988	ASY	49	1410.0	6.928	0.008
	SY	14	606.0		
1987	ASY	43	1252.5	0.277	0.599
	SY	13	343.5		

Table 3. Analysis of variance on nest initiation date.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age	1014.929	1	1014.929	51.150	<0.001
Year	656.344	7	93.763	4.725	<0.001
Age×Year	387.741	7	55.392	2.792	0.007
Error	15079.963	760	19.842		

Clutch Size

Birds lay eggs in discrete numbers, so strictly speaking clutch size is not a continuous variable. Clutch size has been treated historically in the literature as a continuous variable, with mean clutch sizes being reported and analyses being conducted on these values. Even though all of the strict assumptions of the analysis of variance could not be met, due to historical precedence and for purposes of comparison, I treated clutch size in the same manner. I also analyzed these data using the more appropriate distribution-free tests as well.

Average clutch sizes were smaller for SY females throughout the period of observation (1987-1994, Figure 2). Analysis of variance revealed a strong effect of female age on clutch size (Table 4, $F = 28.924$, $P < 0.001$), and although there was a significant year effect ($F = 3.591$, $P = 0.001$), the relationship between SY and ASY clutches remained stable across years (female age $\times$ year interaction, $F = 0.735$, $P =$

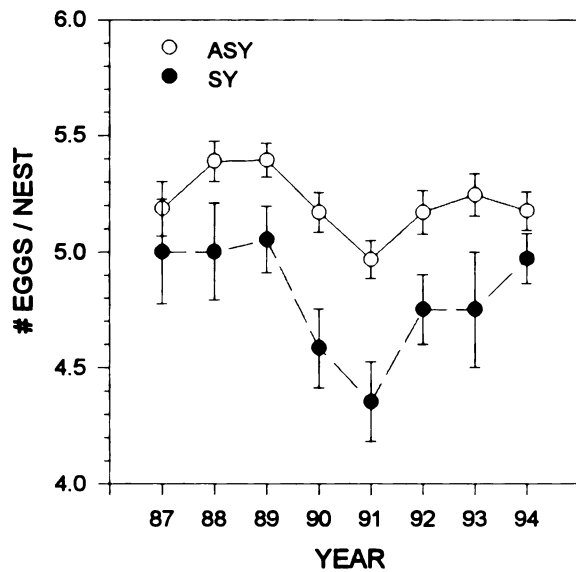


Figure 2. Mean clutch size ($\pm$ S.E.) for SY and ASY females, 1987-1994.

0.642). Overall, clutch sizes for SY females averaged 0.4 eggs/nest less than those observed in ASY females (Tukey's HSD *post-hoc* test, $P < 0.001$).

Because Tree Swallows (Stutchbury and Robertson 1988) as well as other species (*e.g.* Erikstad *et al.* 1985, Hussell 1972, Murphy 1986, Perrins 1965), have been observed to lay

smaller clutches as the season progresses (yet see Conrad and Robertson 1992), and the fact that SY females initiate laying significantly later in the season, on average, than ASY females, the relationship between female age and clutch size may be due, in part, to the time of the season when clutches are initiated. For both SY and ASY females, clutch size decreased significantly with date over all years of the study (SY females,

Table 4. Analysis of variance on clutch size.

Source	SS	DF	MS	F	P
Female Age	16.751	1	16.751	28.924	<0.001
Year	14.558	7	2.080	3.591	0.001
Age×Year	2.982	7	0.426	0.735	0.642
Error	440.139	760	0.579		

Table 5. Analysis of covariance on clutch size, using nest initiation date as the covariate.

Source	SS	DF	MS	F	P
Female Age	5.419	1	5.419	10.339	0.001
Year	11.393	7	1.628	3.105	0.003
Date	42.326	1	42.326	80.756	<0.001
Age×Year	2.736	7	0.391	0.746	0.633
Error	397.813	759	0.524		

slope = -0.048, $R^2 = 0.144$, $n = 119$, $P < 0.001$; ASY females, slope = -0.055, $R^2 = 0.093$, $n = 550$, $P < 0.001$). Controlling for the date of nest initiation over all years in an analysis of covariance (slopes were homogeneous), the effects of female age and year on clutch size both persist strongly (Table 5). Although clutch size is affected significantly by the age of the female, the year, and the date of initiation of egg laying, these factors only explain 16.8% of the variation in clutch size in this population. Other factors, such as location within the plot (Perrins 1965) and habitat (Högstedt 1980, Krebs 1970) have also been shown to affect clutch sizes.

The distribution of clutch sizes (1987-1994) ranged from two to seven, which is typical, although clutch sizes of one and eight eggs have been reported (Turner and Rose 1989). For analysis, clutch sizes were collapsed into adjacent categories of four eggs for clutches of two and three, and six for clutches of seven (Figure 3), because of the low numbers of clutches in some years with two, three, or seven eggs (overall, 41

of 776 clutches or 5.3%). Only ASY females laid clutches of seven eggs ($n = 18$), and, overall, clutches of two and three were rare (2s, $n = 5$; 3s, $n = 18$).

A significant lack of independence in clutch size distribution was observed between SY and ASY females during 1990, 1991 and 1992 (all $P < 0.040$, Table 6).

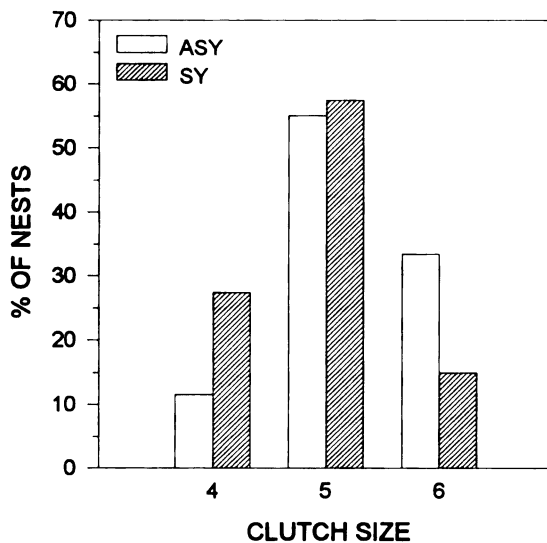


Figure 3. Distribution of clutch sizes. Clutch sizes of two, three and seven are collapsed into adjacent categories and all years are pooled.

Heterogeneity χ^2 testing (Zar 1984, p. 67) revealed that years were homogeneous and thus could be pooled for further analysis (heterogeneity $\chi^2 = 9.04$, $df = 6$, $P > 0.1$). Pooling across years, the resulting 3×2 table shows a significant lack of independence between SY and ASY females with regard to clutch size distribution ($\chi^2 = 35.157$, $df = 1$, $P < 0.001$) and this is evident in Figure 3. Although clutch sizes of five were

the most common for both SY and ASY age classes throughout the study, clutch sizes of four were more prevalent for SY females and clutch size of six were more prevalent for ASY females.

Table 6. Distribution of clutch sizes, 1987-1994. Clutches of two, three, and seven were collapsed into adjacent categories. Female age classes were compared using χ^2 tests.

Year	Age	Frequency of clutch size			χ^2	P
		4	5	6		
1994	ASY	5	49	20	4.934	0.085
	SY	7	21	6		
1993	ASY	10	47	35	1.825	0.402
	SY	7	21	6		
1992	ASY	16	43	35	6.419	0.040
	SY	8	13	3		
1991	ASY	15	56	20	12.811	0.002
	SY	9	8	0		
1990	ASY	16	48	30	8.477	0.014
	SY	8	14	1		
1989	ASY	3	47	36	3.486	0.175
	SY	2	11	4		
1988	ASY	2	27	20	3.068	0.216
	SY	2	9	3		
1987	ASY	5	26	12	3.177	0.204
	SY	4	5	4		

Clutch Size Repeatability

Repeatability is the ratio of the between-individual variance and the total phenotypic variance in a measure (Falconer 1981, Lessells and Boag 1987), and is described by the intraclass correlation coefficient. High repeatability implies little or no change

by individuals over time, whereas low repeatability indicates a greater degree of change by individuals between measurement periods. For individual females aging from SY to ASY ($n = 44$, pooled over years), repeatability of clutch size was low and non-significant ($r = 0.095$, $F_{43,44} = 1.209$, $P = 0.266$). This indicates that there is little correlation between clutch sizes within an individual female during her SY and ASY years. For observations of ASY females encountered two years in a row ($n = 94$, pooled over years), repeatability of clutch size was higher, and the intraclass correlation coefficient was significant ($r = 0.176$, $F_{93,94} = 1.435$, $P = 0.041$). This indicates a higher correlation between clutch sizes produced by individual females between two ASY years than between SY and ASY years, or in other words, less change between years. Repeatabilities calculated for the ASY/ASY dataset were nearly twice as large as the SY/ASY dataset, yet overall, these ASY/ASY values are slightly lower than what has been reported for repeatability of clutch size in other species ($r = 0.23$ in Song Sparrows, $r = 0.248$ in Lesser Snow Geese, both reported in Lessells and Boag (1987), $r = 0.51$ in Great Tits, Perrins and Jones (1975), $r = 0.28$ also in Great Tits, van Noordwijk *et al.* (1980)).

Analysis of mean clutch sizes from the repeatability dataset, comparing SY females moving into the ASY age class ($n = 44$ individuals, pooled over all years), shows that females increased their clutch size with age, on average, 0.182 eggs/nest. This value represents approximately half of the average 0.4 eggs/nest difference observed between the SY and ASY age classes in the entire data set (see Figure 2), yet

mean clutch sizes in this data subset were not different between age classes (SY = 4.773 ± 0.122 eggs/nest, ASY = 4.955 ± 0.121 eggs/nest, paired t-test, $t = 1.159$, $P = 0.253$). For ASY females encountered two years in a row, no change in clutch size was detected (ASY₁ = 5.128 ± 0.077 eggs/nest, ASY₂ = 5.138 ± 0.079 eggs/nest, paired t-test, $t = -0.105$, $P = 0.916$).

Because the data in my study were collected over eight years and there was a significant effect due to year when comparing clutch size between female age classes (Table 4), it is desirable to control for this effect (a portion of the environmental variance) when calculating repeatabilities. This was done by using standard normal deviates of clutch size (Hochachka 1992, Perdeck and Cavé 1992) which were calculated using the equation:

$$CLUTCH\ SIZE_{ADJ} = \frac{INDIVIDUAL\ CLUTCH\ SIZE - YEAR\ MEAN\ CLUTCH\ SIZE}{YEAR\ CLUTCH\ SIZE\ STANDARD\ DEVIATION},$$

where yearly means and standard deviations used in the equation correspond to respective female age groups (SY or ASY) within each year. Following these corrections, repeatability for the SY/ASY group was still very low ($r = 0.044$, $F_{43,44} = 1.093$, $P = 0.385$), whereas the ASY/ASY value was greater and statistically significant ($r = 0.209$, $F_{93,94} = 1.529$, $P = 0.021$).

Even though the mean clutch sizes were not significantly different from one another as individual females aged from SY to ASY, the trend suggests that SY females are more likely to increase clutch size as they age (low r) compared to older females

showing a higher degree of repeatability and very little, if any, change in mean clutch size. This could be explained by several factors, including: 1) females show improvement with age and are better able to produce larger clutches as ASY's one year later, or 2) there is a higher probability of mortality on those females which lay smaller clutches when they are SY compared to SY females that produce larger clutches (Nol and Smith 1987).

Egg Weights

Egg weights were smaller for SY females throughout the study, except in 1993 (Figure 4, Table 7, $F = 35.059$, $P < 0.001$). Weights also showed effects due to the

year of the sample ($F = 19.638$,

$P < 0.001$) as well as a signifi-

cant female age $\times$ year interac-

tion ($F = 2.691$, $P = 0.030$)

which was due to 1993 data

where mean egg weights were

nearly the same for SY and ASY

females.

The effect of individual

females was not included in this

analysis as intraclass correlations

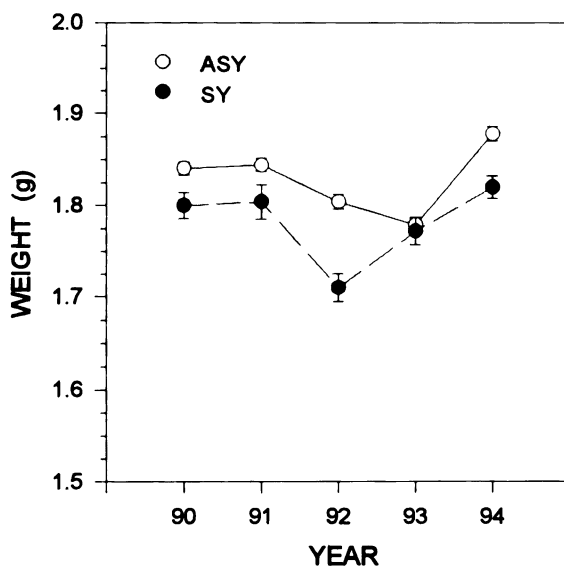


Figure 4. Mean egg weights ($\pm$ S.E.) for SY and ASY females, 1990-1994. Individual eggs are the unit of measure.

during every year showed that the variation among females was greater than the variation within an individual female's clutch of eggs (all $r < 0.72$, all $P > 0.13$, see Winkler 1993). As such, the sample n for the preceding analyses is the number of individual eggs in each female age class.

There is some controversy, however, concerning the use of eggs from the same nest as independent measures, even given the results of the intraclass correlations (Jover, *et al.* 1993). Therefore, two additional approaches were taken, one using mean egg weight for each nest as the unit of measure ($n = 546$ nests, rather than $n = 2789$ eggs), and the second using a nested analysis of variance.

Table 7. Analysis of variance on individual egg weights.

Source	SS	DF	MS	F	P
Female Age	0.837	1	0.837	35.059	<0.001
Year	1.876	4	0.469	19.638	<0.001
Age×Year	0.257	4	0.064	2.691	0.030
Error	66.364	2779	0.024		

Table 8. Analysis of variance on nest mean egg weights.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age	0.151	1	0.151	7.863	0.005
Year	0.385	4	0.096	5.007	0.001
Age×Year	0.046	4	0.012	0.603	0.661
Error	10.292	536	0.019		

Analysis of variance on mean egg weights (Table 8) shows a significant effect due to female age ($F = 7.863$, $P = 0.005$), and year ($F = 5.007$, $P = 0.001$), with no interaction detected. Mean egg weights at SY nests were significantly smaller than means at ASY nests (Tukey's HSD *post hoc* test, $P = 0.005$). These results are generally the same as when individual eggs are used, with some notable exceptions. Using the nest as the unit of measure, standard errors are much larger due to the large drop in sample size; they now overlap in three of the five years of study (Figure 5). Although SY females produce, on average, lower weight eggs in four of five years, t-tests computed by year show significant differences between mean egg weight at SY and ASY nests only during 1992 ($t = 2.343$, $P = 0.021$). In addition, the female age $\times$ year interaction term now becomes nonsignificant.

The second approach, using nested analyses of variance (Table 9), showed a significant effect of the nest (*i.e.* presumably attributes of the individual female) during each year of the study (all $P < 0.001$). Because the factor of the nest accounted for a much greater proportion of the variability in egg weights compared to the factor of female age, significant effects of female age noted earlier were not significant in the

nested models, except during 1992 ($P = 0.028$). Depending upon the year, between 74 and 81 % of the variability in egg weight was attributable to the female that laid the eggs.

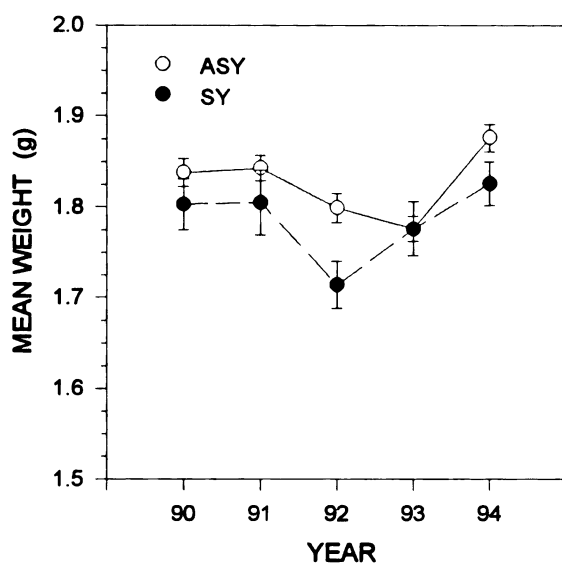


Figure 5. Nest mean egg weights ($\pm$ S.E.) for SY and ASY females.

The relationship between nest mean egg weights and clutch size for SY nests was found to be weak and nonsignificant using regression analysis ($R^2 < 0.01$, $n = 103$, $P = 0.963$). For ASY

nests the relationship was also weak, yet the slope was positive and significant (Nest Mean = $1.740 + 0.016(\text{Clutch Size})$), indicating a trend of increasing egg size with increasing clutch size ($R^2 = 0.009$, $n = 443$, $P = 0.048$).

The relationship between mean egg weight and date of first egg laid (corrected for year) was non-significant for both ASY females ($R^2 < 0.01$, $n = 443$, $P = 0.683$) and SY females ($R^2 = 0.008$, $n = 103$, $P = 0.939$). Because of the lack of relationship between mean egg weight and clutch size or date of first egg, neither of these two measures proved useful as a covariate in an attempt to explain more of the variability in nest mean egg weights.

Table 9. Nested analyses of variance on egg weights by year. Egg weights are nested within the nest (*i.e.* the individual female).

Year	Source	SS	DF	MS	F	P
1990	Female Age	0.097	1	0.097	1.031	0.312
	Nest	10.466	111	0.094	14.542	<0.001
	Error	2.983	460	0.006		
1991	Female Age	0.195	1	0.195	1.797	0.183
	Nest	12.582	116	0.108	17.800	<0.001
	Error	2.821	463	0.006		
1992	Female Age	0.557	1	0.557	4.954	0.028
	Nest	12.153	108	0.113	17.997	<0.001
	Error	2.864	458	0.006		
1993	Female Age	0.000	1	0.000	0.000	0.986
	Nest	8.731	99	0.088	17.538	<0.001
	Error	2.177	433	0.005		
1994	Female Age	0.266	1	0.266	3.073	0.083
	Nest	8.822	102	0.086	13.428	<0.001
	Error	2.763	429	0.006		

Egg Weight Repeatability

Egg weight repeatability of individual SY females moving into the ASY age class ($n = 21$ individuals, pooled over years) was high ($r = 0.737$, $F_{20,21} = 6.907$, $P < 0.001$), which indicates that SY female clutch mean egg weights remain stable with age. Although mean egg weights did increase slightly within individual females aging from SY ($1.775 \pm 0.033\text{g/egg}$) to ASY ($1.806 \pm 0.027\text{g/egg}$), these differences were not significant (paired t-test, $t = -1.477$, $P = 0.155$). Likewise, individual ASY females encountered over two consecutive years ($n = 73$, pooled over years) also showed high repeatability of mean egg weight ($r = 0.830$, $F_{72,73} = 11.847$, $P < 0.001$). Although mean egg weights increased slightly over years ($\text{ASY}_1 = 1.817 \pm 0.017\text{g/egg}$, $\text{ASY}_2 = 1.830 \pm 0.018\text{g/egg}$), again there were no differences in mean egg weight (paired t-test, $t = -1.261$, $P = 0.211$). Other studies have also shown that egg weights are highly repeatable from year to year in the same individual (Ojanen *et al.* 1979, Smith *et al.* 1993). When corrected for yearly variation in mean egg weights (see section on clutch size repeatability), SY/ASY repeatability was slightly lower ($r = 0.696$), and ASY/ASY repeatability increased ($r = 0.891$). Again, there were no significant differences between groups using paired t-tests.

Likelihood To Hatch

Comparing the likelihood of eggs to hatch between female age classes from all of the eggs laid, it was found that significantly greater proportions of eggs hatched

from ASY nests during four of eight years (1989-1992); from SY nests in 1993; and no differences between age classes during 1987, 1988 and 1994 (Table 10).

The likelihood to hatch was not homogeneous over years (heterogeneity χ^2 testing, $\chi^2 = 46.293$, $df = 7$, $P < 0.001$). A test of mutual independence was also rejected ($\chi^2 = 234.84$, $df = 22$, $P < 0.001$) which indicates that some combination of year and female age is influencing the likelihood to hatch. Three tests of partial independence were all rejected (all $P < 0.001$) which further indicates that likelihood to hatch is conditionally dependent upon the factors of year and female age. Because these tests of partial independence were rejected, the most reasonable approach is to consider these data on a yearly basis (Table 10). The significantly lower likelihood of hatching of eggs in SY nests in four of eight years could be due to several reasons, including higher rates of infertility, deficits in incubation behavior, higher rates of predation, or a greater likelihood of nest abandonment.

One of the most striking results is the high likelihood of hatching of eggs for SY females during 1993, which is in sharp contrast to all other years. Population levels of SY females were lowest during 1993 compared to all other years. Although only speculative, if there was differential mortality on young in 1992 resulting in SY individuals nesting in 1993 that were of inherently higher quality in terms of breeding capabilities, this could account for some of the difference observed in hatch rates.

Table 10. Likelihood of eggs to hatch, 1987-1994. Yearly comparisons between SY and ASY females were made using χ^2 tests.

Year	Female Age	# Eggs	# Hatch	# not Hatch	% Hatch	χ^2 / P
1994	ASY	382	336	46	88.0	$\chi^2 = 2.318$
	SY	169	156	13	92.3	$P = 0.128$
1993	ASY	475	379	96	79.8	$\chi^2 = 9.678$
	SY	58	56	2	96.6	$P = 0.002$
1992	ASY	458	356	102	77.7	$\chi^2 = 10.289$
	SY	114	72	42	63.2	$P = 0.001$
1991	ASY	456	371	85	81.3	$\chi^2 = 4.859$
	SY	74	52	22	70.3	$P = 0.027$
1990	ASY	485	404	81	83.3	$\chi^2 = 19.568$
	SY	103	66	37	64.1	$P < 0.001$
1989	ASY	460	338	122	73.5	$\chi^2 = 6.611$
	SY	96	58	38	60.4	$P = 0.010$
1988	ASY	258	227	31	88.0	$\chi^2 = 0.305$
	SY	69	59	10	85.5	$P = 0.581$
1987	ASY	201	137	64	68.2	$\chi^2 = 0.580$
	SY	53	39	14	73.6	$P = 0.446$

Nesting Success Based on Exposure

Using the Mayfield exposure method (Mayfield 1961, 1975), the probabilities of mortality of individual eggs and the incidence of nest failure during egg laying and incubation were compared between SY and ASY females. This method was not used to address mortality of nestlings or nest failure during the time young were in the nest because many of the nests used (nearly all of the SY nests) were manipulated by adding or subtracting young, potentially resulting in a biased sample.

Briefly, exposure is calculated by summing the number of eggdays (for individual eggs) or nestdays (for entire nests) over the time that the nest was under observation. For example, a nest with five eggs which was under observation for 13 days would represent 13 nestdays or 85 eggdays ($5 \text{ eggs} \times 13 \text{ days}$). These exposure values can then be summed within female age classes and probabilities of egg disappearance or nest failure over the time under observation can then be calculated. Comparisons between age classes of females were made on a yearly basis using a χ^2 test (Mayfield 1961, 1975) and, additionally, Z statistics based on maximum likelihood estimates (Hensler and Nichols 1981).

Significantly higher probabilities of losing eggs during egg laying and incubation were recorded for SY females during four of eight years (Table 11, both methods of calculation, all $P < 0.03$). These same four years also showed a significantly lower likelihood of egg hatchability for eggs from SY females (Table 10). During 1993, the probability for egg mortality was significantly lower for SY females calculated by both methods (both $P < 0.004$). This result is noteworthy because 1993 was the same year

Table 11. Probability of egg mortality at SY and ASY nests, 1987-1994, based on the Mayfield exposure method. See text for further explanation.

Year	Female Age	Total Days	# Eggs Lost	Prob. of Egg Loss	Z	P	χ^2	P
1994	ASY	6125	45	0.007	0.342	0.367	0.121	0.728
	SY	2736	22	0.008				
1993	ASY	8512	100	0.012	5.427	<0.001	8.310	0.004
	SY	1026	2	0.001				
1992	ASY	8299	108	0.013	3.338	<0.001	17.019	<0.001
	SY	1839	48	0.026				
1991	ASY	7400	93	0.012	1.929	0.027	5.255	0.022
	SY	1255	26	0.021				
1990	ASY	8705	96	0.011	3.306	<0.001	16.654	<0.001
	SY	2047	46	0.022				
1989	ASY	8294	127	0.015	3.204	<0.001	15.440	<0.001
	SY	1681	49	0.029				
1988	ASY	4373	38	0.009	0.194	0.425	0.039	0.843
	SY	1073	10	0.009				
1987	ASY	3756	97	0.025	1.173	0.121	1.549	0.213
	SY	1164	38	0.033				

when egg weights were not different between SY and ASY females (Figure 4) and SY females showed a significantly greater likelihood to hatch eggs as well (Table 10).

Comparing the probability of nest failure (Table 12) between SY and ASY females, showed that during 1989 and 1992, SY females had a significantly higher rate of nest failure during egg laying and incubation than did ASY females calculated by both methods. During 1993, Z statistics indicated a significantly higher rate of nest mortality

Table 12. Probability of nest failure at SY and ASY nests, 1987-1994, based on the Mayfield exposure method. See text for further explanation.

Year	Female Age	Total Days	# Nests Lost	Prob. of Loss	Z	P	χ^2	P
1994	ASY	1500	0	0.000	1.000	0.159	2.405	0.121
	SY	624	1	0.001				
1993	ASY	1737	6	0.003	2.454	0.007	0.870	0.351
	SY	251	0	0.000				
1992	ASY	1464	9	0.006	2.277	0.011	14.279	<0.001
	SY	253	8	0.032				
1991	ASY	1670	11	0.007	0.785	0.215	0.396	0.529
	SY	289	1	0.003				
1990	ASY	1058	12	0.011	0.180	0.429	0.031	0.860
	SY	484	5	0.010				
1989	ASY	1076	15	0.014	1.715	0.043	5.322	0.021
	SY	219	8	0.037				
1988	ASY	935	3	0.003	0.186	0.425	0.039	0.843
	SY	248	1	0.004				
1987	ASY	707	9	0.013	0.264	0.397	0.065	0.799
	SY	279	3	0.011				

for ASY females ($P = 0.007$), yet the χ^2 test did not ($P = 0.351$). The P values in Tables 11 and 12 indicate clearly that the χ^2 test is the more conservative of the two methods. All other years showed no differences in probability of nest failure between the two female age groups.

These results are in agreement with hatching likelihoods presented earlier and further indicate that SY females have a higher likelihood to lose eggs during the laying and incubation period, yet the incidence of total nest failure was approximately the same for both age classes of females—only during 1989 and 1992 did SY females show a significantly higher rate of nest failure.

PARENTAL CARE

Nest Visitation Rates

Whereas fecundity variables were measured at as many nests as possible, measures of parental care and growth (later section of Results) were obtained from a subset of nests, many of which were manipulated in order to standardize brood sizes to either four or six young, or to eliminate problems with hatching asynchrony (see Methods). These nests are referred to throughout the text as treatment nests.

Although I could not determine the exact age of the males at many treatment nests (unless males were banded as young, which was rare given the very low return rates in this population of less than 1%), I could still test to see if the behavior or effort

of the male at any individual nest was different from that of the known-age female, or was influenced by the behavior or effort of the known-age female. During 1990, four of 14 nests showed lack of independence between frequencies of male and female visits pooled over the course of the entire observation period, when compared to an expected 50/50 ratio of visits. At two of these nests the male visited more frequently, whereas the female visited more frequently at the other two nests. During 1993, none of the 22 nests showed any differences between frequencies of male and females visits over the course of the observation period. The relative proportion of visits made to the nest by males and females was found to be significantly different within the treatment group of ASY nests with four young, where females made a greater number of visits during 24 of 38 observation periods (Wilcoxon test, $Z = -2.975$, $P = 0.003$). For the other three treatment groups, no such differences were found (all $Z > 0.047$, all $P > 0.387$). The adult pairs at SY nests showed a high degree of symmetry with approximately 50% of the observation periods having a greater number of female visits and the other half having a greater number of male visits. Within all four treatment groups, male and female frequencies of visits to the nest were shown to be significantly correlated with one another (Pearson correlations, all $r_p > 0.57$, all $P < 0.001$), so although there were some differences at individual nests, overall, male and female visits were positively and significantly associated. For further analyses of parental care measures by treatment groups, all nests within a treatment group were pooled.

Mean total visits/h (summed female plus male visits), used as an index of parental care, is presented graphically for various treatment group combinations in Figures

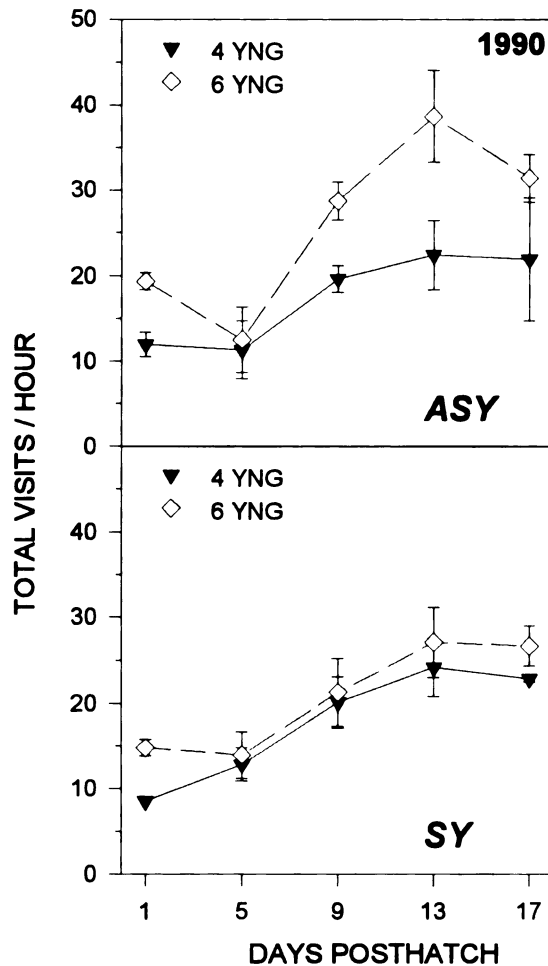


Figure 6. Mean total visits/hour ($\pm$ S.E.) during 1990 at SY and ASY treatment groups.

6-9. During 1990 at ASY nests (top half Figure 6), the number of visits/h was greater at nests with six young when compared to nests with only four young. During 1990 at SY nests (bottom half of Figure 6), the number of visits/h was approximately the same for nests with six young compared to nests with only four young. This shows that adults at SY nests did not increase total visits/h with increased brood size as is evident at ASY nests, suggesting a lower level of parental care on the part of the adults at SY nests. Viewing the same data, but now comparing nests with only four young (top

half Figure 7), no differences in total visits/h are shown between ASY and SY nests.

However, at nests with six young (bottom half Figure 7), a greater number of visits/h

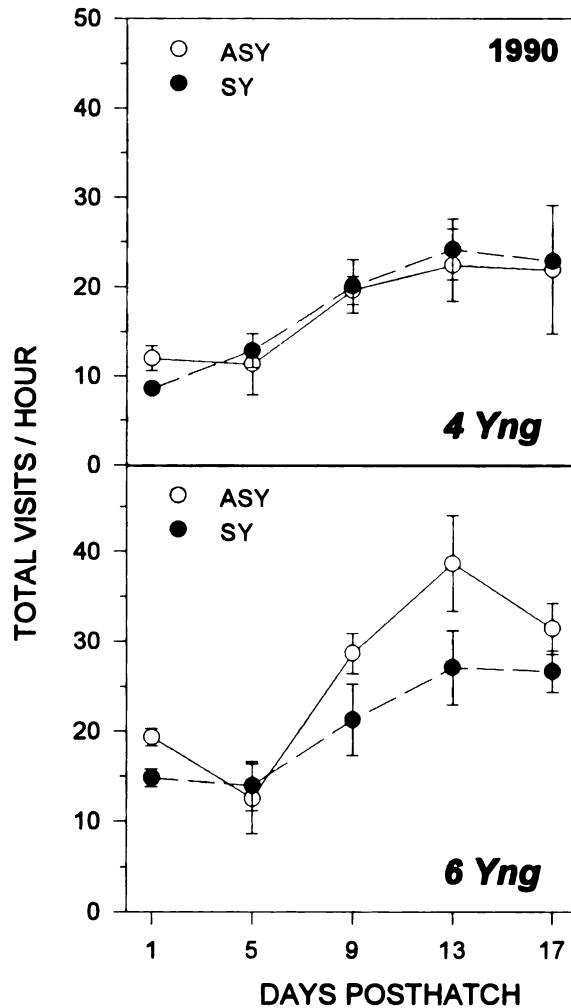


Figure 7. Mean total visits/hour ($\pm$ S.E.) during 1990 at treatment groups with four or six young.

was recorded at ASY nests when compared to SY nests, again suggesting a relatively lower level of parental care on the part of the parents at SY nests with six young.

During 1993, no differences are evident between ASY nests with four or six young (top half Figure 8), whereas at SY nests (bottom half Figure 8), those nests with broods of six young showed higher total visits/h. This is in contrast to results observed in 1990 when visits/h at SY nests with six young were shown to be

less than visits/h at ASY nests. Viewing the same data from a different perspective, total visits/h were approximately equal at ASY and SY nests with four young (top half Figure 9). At nests with six young, however, total visits/h were greater for SY nests when compared to ASY nests (bottom half Figure 9).

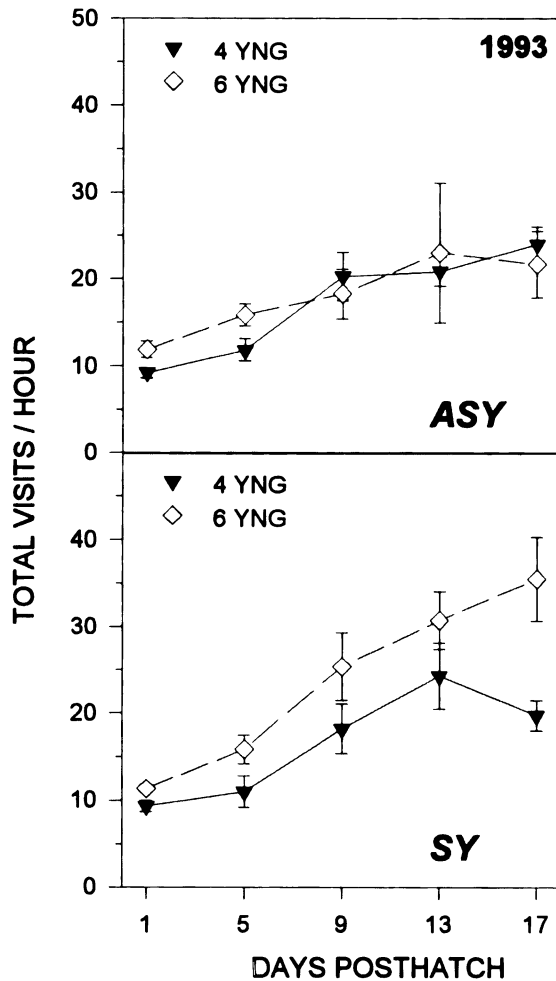


Figure 8. Mean total visits/hour ($\pm$ S.E.) during 1993 at SY and ASY treatment groups.

In order to test statistically for effects due to female age or brood size, repeated measures analysis of variance was used, the repeated measure being visits/h on days 1, 5, 9, 13 and 17 posthatch. Visits/h were represented by total visits/h (female plus male), female visits/h, or male visits/h. Because observations were missing from the data sets during both 1990 and 1993 due to inclement weather or logistical problems, some values were estimated. If only one of five days was missing, the missing observation period value was estimated based on the mean for

that treatment group on that day. If more than one day was missing, the nest was excluded from analyses. For example, if an ASY nest with four young was missing day five of observation, this value was estimated from the other ASY nests with four young which were also observed on day five. Fourteen nests from 1990 and 15 nests from

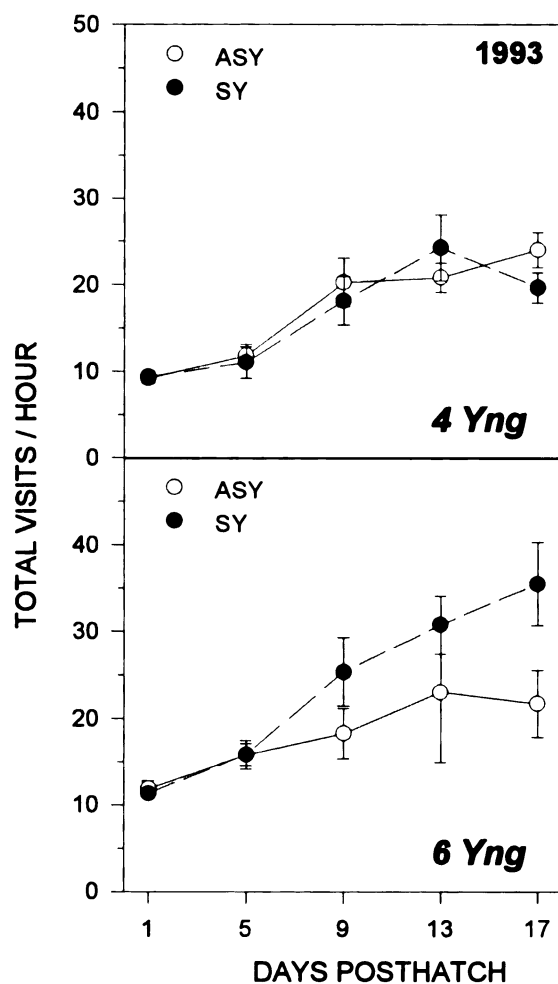


Figure 9. Mean total visits/hour ($\pm$ S.E.) during 1993 at treatment groups with four or six young.

1993 were used in these analyses.

Data were square root transformed in order to meet the assumption of normality.

Results of the repeated measures analysis of variance on total visits/h during 1990 and 1993 using the grouping factors of female age, brood size and year (Table 13) shows a significant effect due to brood size ($F = 18.714$, $P < 0.001$), yet no significant effects due to female age, year, or any of the interaction

terms.

Considering only female visits/h (Table 14), a significant effect due to brood size ($F = 11.003$, $P = 0.003$) and a significant three-way female age $\times$ year $\times$ brood size interaction ($F = 4.418$, $P = 0.048$) were detected. For male visits/h (Table 15), only brood size was significant ($F = 13.109$, $P = 0.002$).

Table 13. Repeated measures analysis of variance on total visits/hour.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.177	1	0.177	0.269	0.609
Year (Y)	0.779	1	0.779	1.186	0.289
Brood Size (B)	12.300	1	12.300	18.714	<0.001
A×Y	2.478	1	2.478	3.770	0.066
A×B	0.010	1	0.010	0.015	0.904
Y×B	0.000	1	0.000	0.000	0.991
A×Y×B	2.436	1	2.436	3.707	0.068
Error	13.803	21	0.657		

Table 14. Repeated measures analysis of variance on female visits/hour.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.008	1	0.008	0.024	0.877
Year (Y)	0.410	1	0.410	1.253	0.276
Brood Size (B)	3.598	1	3.598	11.003	0.003
A×Y	0.776	1	0.776	2.374	0.138
A×B	0.164	1	0.164	0.502	0.486
Y×B	0.173	1	0.173	0.530	0.475
A×Y×B	1.445	1	1.445	4.418	0.048
Error	6.867	21	0.327		

Table 15. Repeated measures analysis of variance on male visits/hour.

Source	SS	DF	MS	F	P
Female Age (A)	0.192	1	0.192	0.262	0.614
Year (Y)	0.324	1	0.324	0.442	0.513
Brood Size (B)	9.594	1	9.594	13.109	0.002
A×Y	1.969	1	1.969	2.691	0.116
A×B	0.371	1	0.371	0.507	0.484
Y×B	0.211	1	0.211	0.288	0.597
A×Y×B	1.153	1	1.153	1.575	0.223
Error	15.369	21	0.732		

Although comparison of Figures 6-9 seems to suggest that female age (*i.e.* nest type characterized by the age of the female) and year may be important factors, their influence was too small to be detected due to the high variability in the frequency of visits over time. Brood size (four versus six young) was the most important factor influencing the number of visits made to the nest by parents in this design. This was expected, since if equal provisioning of individual young is the norm, then visits/h would be higher at nests with six young. In order to control for this factor, each brood size was considered separately in the following analyses.

Considering only nests with four young (Table 16), repeated measures analysis of variance on the dependent variables of total, female or male visits/h, shows that no significant effects due to female age or year were detected in any of the models. This suggests that across both years (1990 and 1993) and both treatment groups (SY and ASY nest types), the level of parental care, as indexed by the number of visits made to

Table 16. Repeated measures analysis of variance on total, female and male visits/hour at nests with four young only.

Total visits/hour					
Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.123	1	0.123	0.150	0.707
Year (Y)	0.363	1	0.363	0.443	0.522
A×Y	0.000	1	0.000	0.000	0.992
Error	7.381	9	0.820		
Female visits/hour					
Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.046	1	0.046	0.167	0.692
Year (Y)	0.023	1	0.023	0.084	0.779
A×Y	0.047	1	0.047	0.172	0.688
Error	2.457	9	0.273		
Male visits/hour					
Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.501	1	0.501	0.586	0.464
Year (Y)	0.483	1	0.483	0.565	0.471
A×Y	0.050	1	0.050	0.058	0.815
Error	7.688	9	0.854		

the nest, is uniform at nests with four young. These results are graphically represented in the top halves of Figures 7 and 9.

Considering only nests with six young (Table 17), a different picture emerges. No significant effects due to female age or year were detected, yet a significant female age × year interaction was detected for total visits/h ($F = 10.147$, $P = 0.008$), female

visits/h ($F = 6.522$, $P = 0.025$), and male visits/h ($F = 5.296$, $P = 0.040$). These results from treatment nests with six young indicate a significantly different response on the part of parents at SY vs. ASY nests between the two years of observation. This is evident in the bottom halves of Figures 7 and 9 where total visits/h at nests with six young is highest at ASY nests during 1990, yet highest at SY nests in 1993. During 1990, at nests with six young, total visits/h was significantly higher at ASY nests (one-way repeated measures analysis of variance, $F = 7.657$, $P = 0.033$). During 1993, however, even though graphically visits/h were greater at SY nests, no statistically significant differences were detected ($F = 4.125$, $P = 0.089$).

Another approach is to assess parental care activity on a daily basis. Although this analysis could be conducted on all five days of observation, day 13 was chosen because it represents the time of maximum number of visits made to most nests and the assumption was made that any differences between treatment groups would be accentuated at this time when the parents were presumably working the hardest. Analysis of variance (Table 18) on the dependent variable of total visits/h detected a significant effect due to the number of young in the nest ($F = 5.369$, $P = 0.029$), yet no other factors or interaction terms were significant. Post-hoc comparisons showed that overall, rates of visitation by adults at ASY nests with six young did not differ on day 13 compared to adults at SY nests with six young ($P > 0.9$). The same result was shown at nests with four young ($P > 0.9$). Similar results of significant effects of brood size

Table 17. Repeated measures analysis of variance on total, female and male visits/hour, for nests with six young only.

Total visits/hour					
Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.057	1	0.057	0.107	0.749
Year (Y)	0.422	1	0.422	0.788	0.392
A×Y	5.430	1	5.430	10.147	0.008
Error	6.421	12	0.535		
Female visits/hour					
Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.135	1	0.135	0.367	0.556
Year (Y)	0.616	1	0.616	1.677	0.220
A×Y	2.397	1	2.397	6.522	0.025
Error	4.410	12	0.368		
Male visits/hour					
Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.016	1	0.016	0.025	0.876
Year (Y)	0.007	1	0.007	0.010	0.920
A×Y	3.390	1	3.390	5.296	0.040
Error	7.680	12	0.640		

were recorded for female visits/h, yet for male visits/h no significant main effects were detected.

In summary, the analyses show that brood size most strongly influenced the number of visits made to the nest by parents, which was expected given the fact that only two brood sizes were used in the experimental design. At nests with four young, parents maintained a fairly even rate of visitation across treatment groups and years. At

nests with six young, significantly higher rates of visitation were recorded at ASY nests in 1990 ($P = 0.033$), yet during 1993 higher rates were observed at SY nests although the comparison was marginally non-significant ($P = 0.089$).

Table 18. Analysis of variance on total visits/hour. Data from day 13 posthatch only.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	1.794	1	1.794	0.025	0.876
Year (Y)	80.166	1	80.166	1.111	0.302
Brood Size (B)	387.421	1	387.421	5.369	0.029
A×Y	223.258	1	223.258	3.094	0.091
A×B	34.084	1	34.084	0.472	0.498
Y×B	47.140	1	47.140	0.653	0.427
A×Y×B	160.045	1	160.045	2.218	0.149
Error	1803.811	25	72.152		

Weight of Food Delivered to Young

All bolus collection data were log transformed to meet the assumption of normality. Regression analyses on data collected from all three years (1989-1991) showed that bolus weights increased significantly with the age of the young (Table 19). In addition, slopes of the regression equations were found to be homogeneous, with 1989 having the largest boluses and 1991 the smallest (Figure 10). Nested analysis of covari-

ance (Table 20) revealed a significant effect of year ($F = 6.476$, $P = 0.004$) and nest ($F = 1.785$, $P = 0.005$) after controlling for age of the young ($F = 28.450$, $P < 0.001$), yet no significant effect due to nest type (*i.e.* SY or ASY nest). Together these factors accounted for 31.5% of the variability in bolus weight delivered. Because data collection protocols were slightly different between years (see Methods), I also analyzed years separately and found no effect due to nest type (SY or ASY nest) after controlling for age of young, a significant covariate.

Table 19. Linear regression analyses on log transformed bolus weights. Independent variable was days posthatch. Probability values indicate slopes significantly different from zero.

Year	<i>n</i>	Slope	R^2	<i>P</i>
1989	87	0.091	0.221	<0.001
1990	176	0.064	0.090	<0.001
1991	136	0.057	0.128	<0.001

During 1991, using the blind observational system developed for the purpose (see Methods), I was able to distinguish between male and female boluses at six nests, three of which were SY nests and three ASY nests. Mean bolus weight, pooled over sexes, nests, and days of observation, was lower at SY nests (0.025 ± 0.002 g), when compared to ASY nests (0.028 ± 0.001 g). Although one-way analysis of variance detected significant differences in bolus weight ($F = 6.259$, $P = 0.014$), the nest type (SY vs. ASY nest) explained only 4.5% of the variability in bolus weight. However,

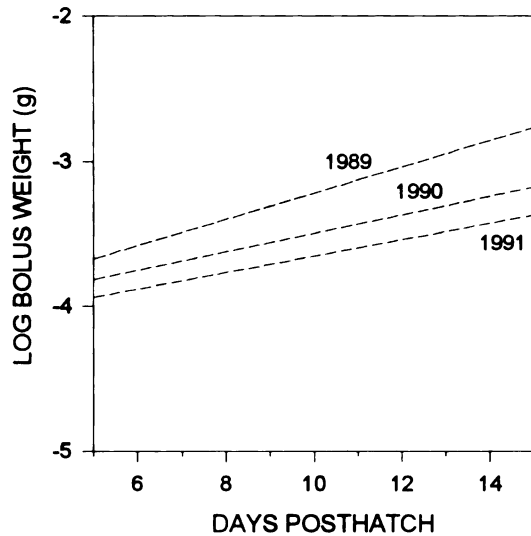


Figure 10. Regression lines representing log of bolus weights increasing over time. All slopes were homogeneous and significantly different from zero.

after controlling for age of the young using analysis of covariance, the nest type factor became nonsignificant.

Comparing male bolus weights only, no differences between males at SY nests were detected when tested against males at ASY nests ($F = 0.748$, $P = 0.392$), again controlling for age of the young. Although mean female bolus weight was larger for

ASY females (0.026 ± 0.001 g) than SY females (0.022 ± 0.002 g), they were not significantly different ($F = 0.744$, $P = 0.392$) after controlling for age of the young.

Whereas female bolus weight increased significantly over time with the age of the young ($n = 69$, $\text{Log Bolus Weight} = -4.375 + 0.067(\text{Days})$, $P < 0.001$), male bolus weight increases over time were smaller and not significant ($n = 43$, $\text{Log Bolus Weight} = -3.783 + 0.022(\text{Days})$, $P = 0.363$).

Table 20. Nested analysis of variance on log transformed bolus weights. Covariate was days posthatch.

Source	SS	DF	MS	F	P
Female Age	0.064	1	0.064	0.177	0.715
Year	3.735	2	1.867	6.476	0.004
Age×Year	0.720	2	0.360	1.248	0.299
Nest	10.380	36	0.288	1.785	0.005
Days Posthatch	4.597	1	4.597	28.450	<0.001
Error	57.518	356	0.162		

GROWTH OF YOUNG

Growth Curves

Graphical representations of the mean measures of weight and wing lengths increasing over time for the four treatment groups during 1990 are presented in Figures 11 and 12 and values for 1993 are shown in Figures 13 and 14. For clarity, the figures are shown without standard errors, which are very small. Each mean is represented by 12-36 young depending upon the treatment group and year. During 1990, the topmost

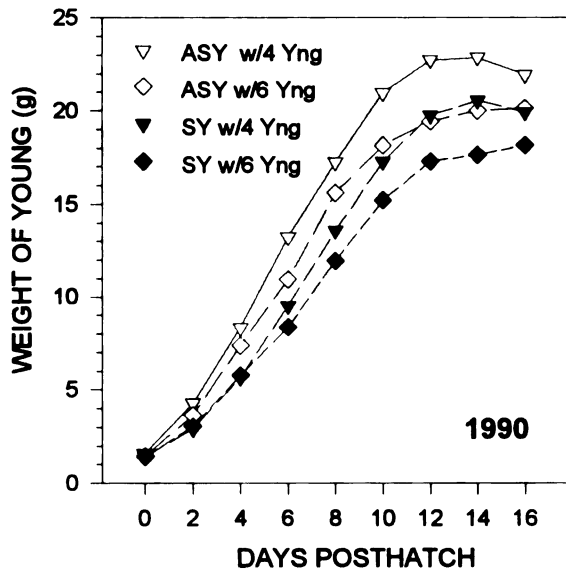


Figure 11. Increase in nestling weight over time during 1990 for all four treatment groups.

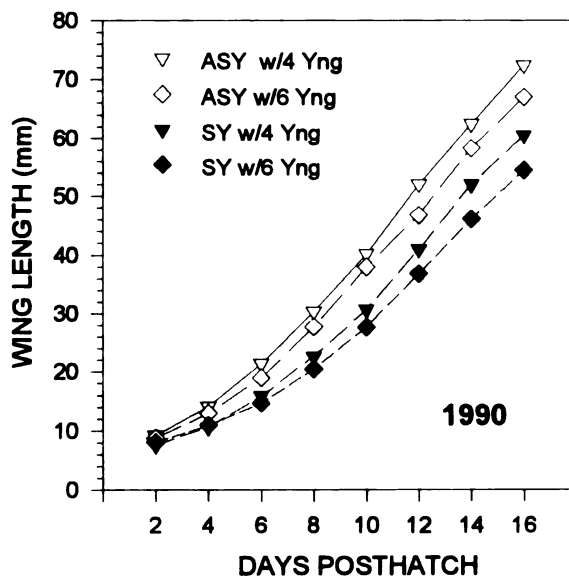


Figure 12. Increase in nestling wing length over time during 1990 for all four treatment groups.

curve (open triangles) for both weight (Figure 11) and wing (Figure 12) measures represents ASY nests with four young, whereas the bottom curve (filled diamond) in each 1990 figure represents SY nests with six young. It appears as though nestlings during 1990 in ASY nests with four young are growing most rapidly and reach a higher final measure than do the nestlings in SY nests with six young which do more poorly. The other two treatment groups, ASY nests with six young and SY nests with four young, show intermediate values.

During 1993, for the variable of weight (Figure 13), the topmost curve represents SY nests with four young and the lower

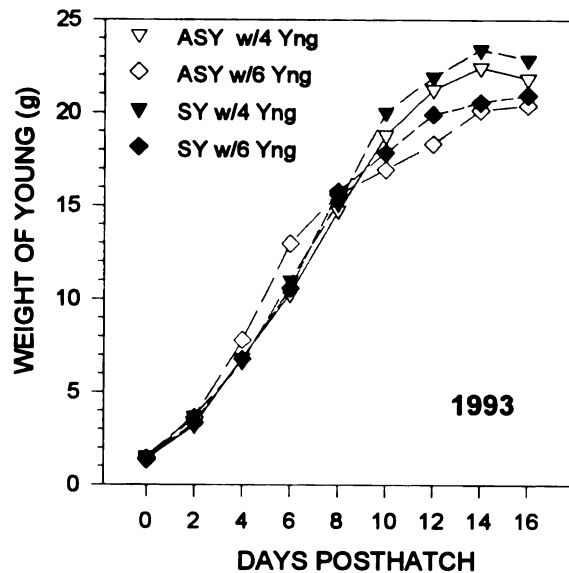


Figure 13. Increase in nestling weight over time during 1993 for all four treatment groups.

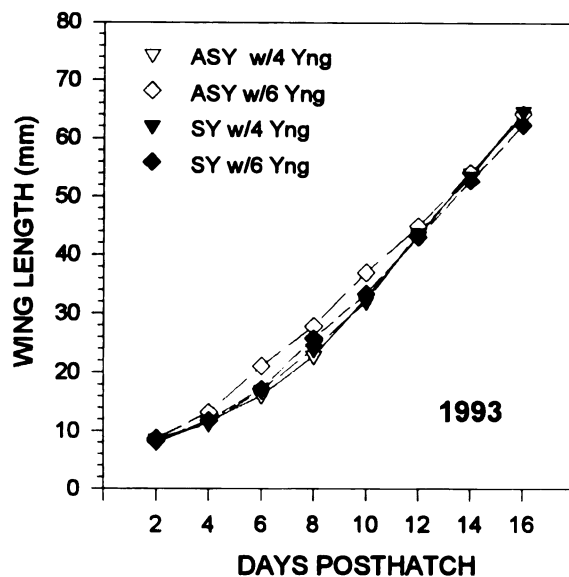


Figure 14. Increase in nestling wing length over time during 1993 for all four treatment groups.

curve ASY nests with six young.

For the variable wing length (Figure 14), however, there is very little visual difference between the four treatment groups. Detailed analyses on nestling weights and wing lengths follow.

Individual nestling growth measures were fit to growth models (Ricklefs 1967, 1983) in a non-linear curve fitting routine in SYSTAT® (Wilkinson 1992).

Highest overall R^2 values were obtained by using the logistic model for weight and the exponential model for wing length.

The same procedures have been used for Tree Swallows by Zach and Mayoh (1982) and Beaver *et al.* (1994).

Variables used in the following analyses include the weight growth constant which is estimated by the logistic model and the wing growth constant which is estimated by the exponential model. Also considered were maximum weights and maximum wing lengths, both of which have been shown to be less variable than fitted parameters from the non-linear growth models (Zach 1988).

Weight: Fitted Growth Constants

Mean weight growth constants (Figure 15) were slightly higher for 1993 measures in three of the four treatment groups compared to 1990 values, yet standard errors are large and overlapped in all combinations of treatment groups and years. Analysis of variance revealed no significant effects due to female age, year or brood size (Table

21), and there were no significant interactions, yet this model only explains a small amount of the variability in the weight growth constant ($R^2 = 0.035$). Using a nested analysis of variance model (Table 22) which includes the factors of female age, year, brood size and nest (nested within all three of the first factors), plus

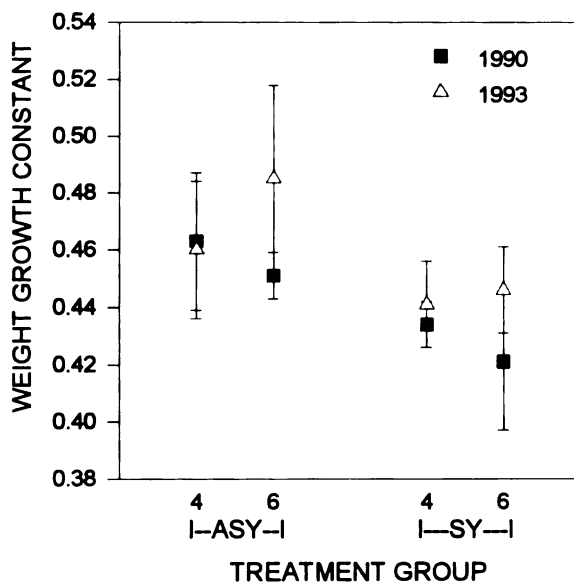


Figure 15. Mean weight growth constants ($\pm$ S.E.) during 1990 and 1993 for all four treatment groups.

Table 21. Analysis of variance on weight growth constants, $R^2 = 0.035$.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.032	1	0.032	3.506	0.063
Year (Y)	0.010	1	0.010	1.075	0.301
Brood Size (B)	0.000	1	0.000	0.005	0.944
A×Y	0.000	1	0.000	0.000	0.995
A×B	0.001	1	0.001	0.121	0.728
Y×B	0.007	1	0.007	0.803	0.371
A×Y×B	0.001	1	0.001	0.090	0.764
Error	1.446	160	0.009		

interaction terms, shows significant effects due to the nest ($F = 13.272$, $P < 0.001$) as well as female age ($F = 349.384$, $P = 0.034$), with no significant interactions. Mean growth constants were lower at nests with SY females compared to nests with ASY females (see Figure 15). This nested model explains a large amount of the variability in the dependent variable of weight growth constant ($R^2 = 0.781$). In other words, much of the variability shown in the growth constant values for weight are due to the individual nest from which they were obtained.

Although growth constants were normally distributed, some outliers were evident in stem/leaf plots. With three outliers removed, the female age factor in a nested model becomes non-significant ($F = 4.072$, $P = 0.293$). All three outliers represented very high growth constant values from two ASY nests with six young during 1993. These three nestlings all showed rapid growth for several days, quickly reaching as-

ymptotic weights which were very low, indicating poor overall growth. Generally, high growth constants translate into high quality growth, yet in these cases the opposite was true.

Table 22. Nested analysis of variance on weight growth constants, $R^2 = 0.747$.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	0.044	1	0.044	349.384	0.034
Year (Y)	0.019	1	0.019	0.497	0.487
Brood Size (B)	0.000	1	0.000	0.001	0.979
Nest	1.067	28	0.038	13.272	<0.001
A×Y	0.000	1	0.000	0.003	0.955
A×B	0.004	1	0.004	21.740	0.658
Y×B	0.014	1	0.014	0.357	0.555
A×Y×B	0.000	1	0.000	0.004	0.948
Error	0.379	132	0.003		

Weight: Maximum Values Attained

Weight asymptotes were also calculated from the logistic models, yet the results were very similar to the maximum values of weight which are reported here. The maximum values were also slightly less variable, a result also reported by Zach (1988) in Tree Swallows.

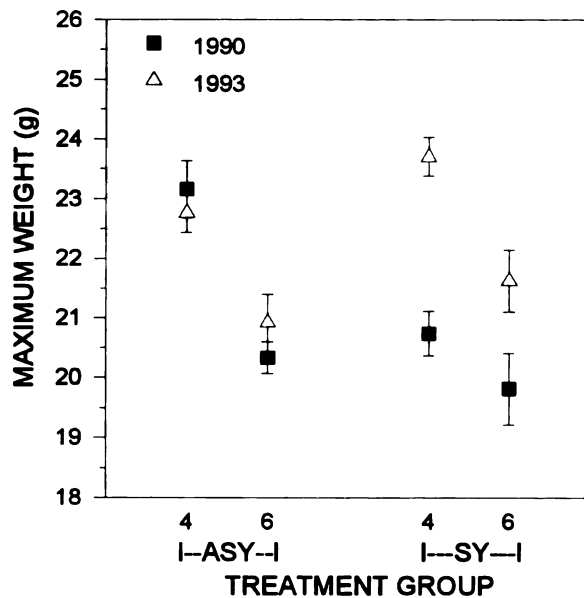


Figure 16. Mean maximum weight ($\pm$ S.E.) attained by nestlings during 1990 and 1993 for all four treatment groups.

Mean maximum values of weight attained during the period of measurement show higher values for three of the four treatment groups during 1993 (Figure 16). Results of an analysis of variance model including the factors of female age, year, brood size, and interaction terms (Table 23) showed significant effects due to year ($F = 13.106$, $P < 0.001$) and brood size ($F = 31.308$, $P <$

0.001). The female age $\times$ year interaction term was also significant. Using a nested analysis of variance model (Table 24) which further included the factor nest (nested within all three of the first factors), plus interaction terms, shows significant effects of year ($F = 5.099$, $P = 0.032$), brood size ($F = 410.304$, $P = 0.031$) and nest ($F = 3.136$, $P < 0.001$). The female age $\times$ year interaction term was also significant. This interaction is due to mean maximum values at ASY nests being approximately equal between 1990 and 1993, whereas mean maximum values were higher for SY nests during 1993 than 1990 (see Figure 16). The nested model also explains a greater

amount of variability ($R^2 = 0.569$) than the unnested model ($R^2 = 0.283$). In addition, results changed very little with the exclusion of two outliers.

Table 23. Analysis of variance on maximum weights attained by nestlings, $R^2 = 0.283$.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	3.955	1	3.955	0.893	0.346
Year (Y)	58.058	1	58.058	13.106	<0.001
Brood Size (B)	138.697	1	138.697	31.308	<0.001
A×Y	49.067	1	49.067	11.198	0.001
A×B	6.441	1	6.441	1.454	0.230
Y×B	0.056	1	0.056	0.013	0.911
A×Y×B	10.767	1	10.767	2.430	0.121
Error	708.805	160	4.430		

Table 24. Nested analysis of variance on maximum weights attained by nestlings, $R^2 = 0.569$.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	3.305	1	3.3305	0.071	0.834
Year (Y)	51.564	1	51.564	5.099	0.032
Brood Size (B)	137.337	1	137.337	410.304	0.031
Nest	283.129	28	10.122	3.136	<0.001
A×Y	46.565	1	46.565	4.605	0.041
A×B	7.774	1	7.774	0.690	0.559
Y×B	0.335	1	0.335	0.033	0.857
A×Y×B	11.274	1	11.274	1.115	0.300
Error	425.676	132	3.225		

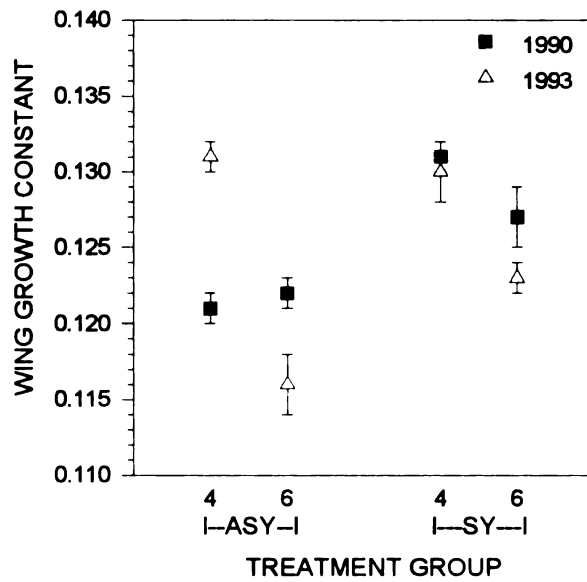


Figure 17. Mean wing length growth constants ($\pm$ S.E.) during 1990 and 1993 for all four treatment groups.

Wing Length: Fitted Growth

Constants

Mean values for wing growth constants during the period of measurement show higher values for three of the four treatment groups during 1990 (Figure 17). Results of an analysis of variance model including the factors of female age, year, brood size, and appropriate interaction

terms (Table 25) showed significant effects due to female age ($F = 23.110$, $P < 0.001$) and brood size ($F = 32.793$, $P < 0.001$). Three of the four interaction terms

Table 25. Analysis of variance on wing growth constants, $R^2 = 0.365$.

Source	SS	DF	MS	F	P
Female Age (A)	0.001	1	0.001	23.110	<0.001
Year (Y)	0.000	1	0.000	0.033	0.857
Brood Size (B)	0.001	1	0.001	32.793	<0.001
A×Y	0.000	1	0.000	3.967	0.048
A×B	0.000	1	0.000	0.479	0.490
Y×B	0.001	1	0.001	17.483	<0.001
A×Y×B	0.000	1	0.000	9.061	0.003
Error	0.007	160	0.000		

were also significant.

Using a nested analysis of variance model (Table 26) which includes the factors of female age, year, brood size and nest (nested within all three of the first factors), plus interaction terms, shows a significant effect due to nest ($F = 6.052$, $P < 0.001$) and a significant year $\times$ brood size interaction. This interaction is due to mean values

Table 26. Nested analysis of variance on wing growth constants, $R^2 = 0.722$.

Source	SS	DF	MS	F	P
Female Age (A)	0.001	1	0.001	6.676	0.235
Year (Y)	0.000	1	0.000	0.058	0.811
Brood Size (B)	0.001	1	0.001	1.586	0.427
Nest	0.004	28	0.000	6.052	<0.001
A $\times$ Y	0.000	1	0.000	1.231	0.227
A $\times$ B	0.000	1	0.000	0.126	0.783
Y $\times$ B	0.001	1	0.001	6.478	0.017
A $\times$ Y $\times$ B	0.000	1	0.000	2.849	0.103
Error	0.003	132	0.000		

at nests with four young being greater in 1993, whereas means were greater during 1990 at nests with six young (see Figure 17). This nested model explains greater than 70% of the variability in the wing growth constant values ($R^2 = 0.722$); the unnested model explains less ($R^2 = 0.365$). Although several outliers were detected by viewing the distribution of the wing growth constant data, all of the individual nestlings

exhibited slow but steady growth throughout the observation period. None was removed for further analyses.

Wing Length: Maximum Values Attained

Growth measures were only recorded through 16 days posthatch and wing feathers are still growing at that time. As such, the maximum wing length attained during this time period represents an index of potential wing size at the time of fledging, which occurs within several days, rather than an absolute measure of maximum wing length.

Wing maximum values were squared to render the data set normal. Mean

maximum values attained for wing measurements were greater during 1990 at ASY nests and greater during 1993 at SY nests (Figure 18). Whereas marked differences are shown between treatment groups during 1990, no differences were shown during 1993.

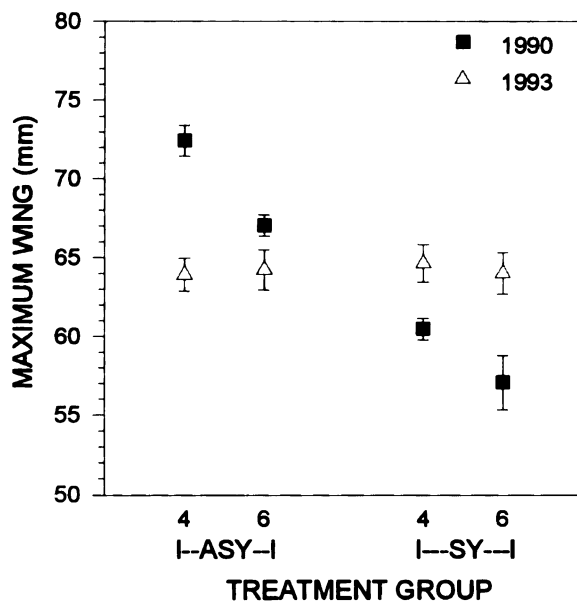


Figure 18. Mean maximum wing length ($\pm$ S.E.) attained by nestlings during 1990 and 1993 for all four treatment groups.

An analysis of variance model including the factors of female age, year, brood size, and appropriate interaction terms (Table 27), showed significant effects due to female age ($F = 33.915$, $P < 0.001$), brood size ($F = 5.793$, $P = 0.017$), and one

Table 27. Analysis of variance on maximum wing length attained by nestlings. Data were transformed by squaring and values for SS and MS are presented $\times 10^{-5}$ for clarity. $R^2 = 0.297$.

Source	SS	DF	MS	<i>F</i>	<i>P</i>
Female Age (A)	1079.517	1	1079.517	32.503	<0.001
Year (Y)	0.101	1	0.101	0.003	0.956
Brood Size (B)	196.072	1	196.072	5.904	0.016
A×Y	1181.930	1	1181.930	35.587	<0.001
A×B	2.566	1	2.566	0.077	0.781
Y×B	171.915	1	171.915	5.176	0.024
A×Y×B	19.944	1	19.944	0.600	0.440
Error	5314.043	160	33.213		

interaction term. Using a nested analysis of variance model (Table 28) which further included the factor of nest (nested within all three of the first factors), plus interaction terms, shows a significant effect due to nest ($F = 7.501$, $P < 0.001$) and a significant female age $\times$ year interaction. This interaction is due to higher overall ASY nest means during 1990, whereas overall SY nest means were higher during 1993 (see Figure 18). This nested model explains a much greater proportion of the variability in maximum wing values ($R^2 = 0.729$) when compared to the unnested model ($R^2 = 0.297$). No outliers were detected in the maximum wing length data set.

It is apparent from the results of the nested models presented above that the nest effect is one of the most important factors influencing growth of young in this system. While the factors of female age, year and brood size help explain some of the variabil-

Table 28. Nested analysis of variance on maximum wing length attained by nestlings. Data were transformed by squaring and values for SS and MS are presented $\times 10^{-5}$ for clarity. $R^2 = 0.729$.

Source	SS	DF	MS	F	P
Female Age (A)	1074.965	1	1074.965	0.905	0.516
Year (Y)	0.820	1	0.820	0.007	0.932
Brood Size (B)	220.581	1	220.581	1.422	0.444
Nest	3141.505	28	112.197	6.817	<0.001
A×Y	1188.281	1	1188.281	10.591	0.003
A×B	1.359	1	1.359	0.065	0.841
Y×B	155.157	1	155.157	1.383	0.250
A×Y×B	20.854	1	20.854	0.186	0.670
Error	2172.539	132	16.459		

ity in the dependent variables and are sometimes significant in the non-nested models, values of R^2 nearly double with the addition of the nested factor to the models.

RELATIONSHIPS BETWEEN PARENTAL CARE AND GROWTH OF YOUNG

The prediction that young at SY nests, and especially at those nests with six young, would exhibit lower rates of growth or overall poorer growth and corresponding

lower levels of parental care was assessed using graphical as well as direct and indirect statistical approaches.

Weight of nestlings prior to fledging has been shown to be an important factor influencing survival of young during the post-fledging period (Hochachka and Smith 1991, Magrath 1991, Perrins 1965). Condition of young at fledging is likely even more critical in Tree Swallows given that fact that there is little evidence of post-fledging parental care (Turner and Rose 1989, yet see comments by Wheelwright *et al.* 1991). Because of the relationship between overall size and subsequent survival, it is important to determine the strength of correspondence between the levels of parental care delivered and measures of growth of young.

During 1990, mean total visits/young/h over the five days of observation (top half Figure 19) showed very similar results at three of four treatment groups, the exception being at SY nests with six young, where young were visited at a much lower rate, on days 9, 13 and 17. This lower rate of visitation (*i.e.* feeding) amounted to approximately one to two less visits per young per hour at these nests compared to all other treatment groups.

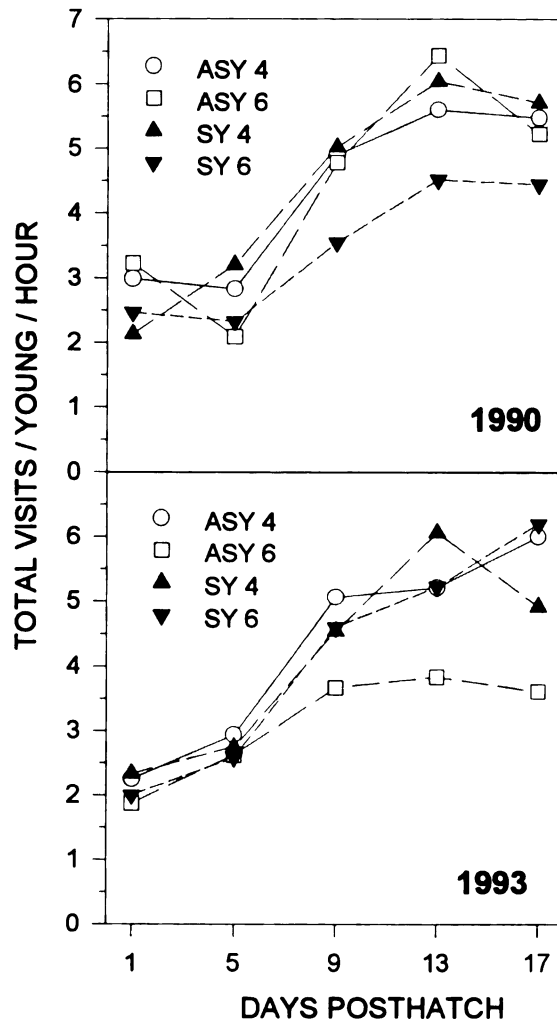


Figure 19. Total visits/young/hour during 1990 and 1993 at all four treatment groups.

Mean weight growth

constants (Figure 15), however, showed high variability and no significant differences between any of the four treatment groups were recorded during 1990 (*post-hoc* tests, all pairs comparisons with Bonferroni adjustments, all $P > 0.8$). Mean maximum weight values for weight during 1990 (Figure 16) were significantly higher for young at ASY nests with broods of four compared to the other three treatment groups (all $P < 0.05$), yet the number of visits/young/h made by adults at this treatment group

appeared to be no different than from the number made to ASY nests with six young or to SY nests with four young. Mean values for wing growth constants (Figure 17) were significantly larger during 1990 at SY nests with four young when compared to ASY nests with four young ($P = 0.007$) or ASY nests with six young ($P = 0.003$), yet these differences are not reflected in visits/young/h which are approximately the same for

these three treatment groups. Mean values of maximum wing length attained (Figure 18) were significantly smaller at SY nests with six young when compared to ASY nests with four young ($P < 0.001$) or ASY nests with six young ($P < 0.001$), and this relationship corresponds to the values for visits/young/h. In contrast, maximum wing lengths did not differ between SY nests with four or six young ($P = 0.743$), yet visits/young/h at SY nests with four young were high compared to SY nests with six young.

During 1993, mean total visits/young/h over the five days of observation (bottom half Figure 19) showed very similar results at three of four treatment groups, this time the exception being at ASY nests with six young, where young were visited at lower rates on days 9, 13 and 17 compared to the other three treatment groups. This lower rate of visitation (*i.e.* feeding) amounted to approximately one to two less visits per young per hour at these nests compared to all others. Mean weight growth constants (Figure 15) during 1993, which were highly variable, showed no significant differences between the treatment groups (*post-hoc* tests, all pairs comparisons with Bonferroni adjustments, all $P > 0.9$), even though visitation rates were much lower at ASY nests with six young. Mean maximum weights (Figure 16) were significantly lower for ASY nests with six young when compared to ASY nests with four young ($P = 0.005$) or SY nests with four young ($P < 0.001$), yet not when compared to SY nests with six young ($P > 0.9$). For wing length measures in 1993, calculated growth constants (Figure 17) were significantly lower for ASY nests with six young compared to the other three

treatment groups (all $P < 0.005$). This corresponds very well to visitation rates which were lowest for ASY nests with six young and approximately equal for the other three treatment groups (Figure 19). Maximum wing length attained in 1993 shows no differences between any of the four treatment groups (all $P > 0.9$, Figure 18), even though visitation rates were lowest at ASY nests with six young, and essentially the same at the other three treatment groups.

There are difficulties inherent in comparing the relationships between parental age and growth statistically due to the non-independent nature of some of the measurements involved. For example, parental care assessed as visits/h during five observation periods is not independent over time since day 5 activity is likely influenced by day 1 activity and so on. Although some have argued that these measures are independent (*e.g.* Lombardo 1991) and have treated them as such, this is not the case, as days 1, 5, 9, 13 and 17 are clearly repeated measures on the same subject. In addition, growth is described using an index for many of the above analyses (*i.e.* growth constants calculated from the logistic equations), and it is difficult to relate an index, which is a single measure, to parental care factors measured over time.

In an attempt to address the issue of non-independent measures, I computed an index of parental care for each nest by summing visits/h over the five observation periods. Missing data were dealt with in the same manner as described earlier in the parental care section for the repeated measures analysis of variance. Fourteen nests from 1990 and 15 nests from 1993 were used in the following analyses. I also com-

puted a new response variable of growth for each nest based on the average for all nestlings. For example, weight growth constants for all nestlings in a nest were averaged to produce a nest average growth constant which was used in the following analyses. Using multiple linear regression, the dependent or response variables of nest mean growth constants and nest mean maximum values attained (for both weight and wing length) were tested for strength of relationships to the independent or explanatory variables, female age, year, brood size, and indices of parental care (delineated by total, female or male visits/h). Three models were run for each growth measure and included all of the explanatory variables above plus one of the parental care indices (total, female, or male visits/h).

Weight growth constants were not significantly related to any of the explanatory variables used in the regression models (Table 29) which explained only approximately 10% of the variability in the calculated weight growth constant (R^2 range = 0.082-0.111). For maximum weight attained (Table 29), the factors of year and number of young were significant in all three models (R^2 range = 0.480 to 0.487).

Wing growth constants (Table 30) were significantly related to age of female and number of young for the models using total visits/h or female visits/h (R^2 = 0.352 and 0.431, respectively), and to female age for the model using male visits/h (R^2 = 0.390). Maximum wing values attained (Table 30) were significantly related to female age and number of young for the model including total visits/h (R^2 = 0.453), to female age only for the model including female visits/h (R^2 = 0.385), and to female age,

Table 29. Multiple linear regression of nest mean growth variables: Weight growth constants and maximum weights.

Dependent variable: Nest Mean Weight Growth Constant					
$R^2 = 0.086$		$R^2 = 0.082$		$R^2 = 0.111$	
Model	<i>P</i>	Model	<i>P</i>	Model	<i>P</i>
Female Age	0.168	Female Age	0.180	Female Age	0.147
Year	0.715	Year	0.798	Year	0.718
Brood Size	0.628	Brood Size	0.973	Brood Size	0.451
Total Visits/h	0.644	Female Visits/h	0.746	Male Visits/h	0.352

Dependent variable: Nest Mean Weight Maximum Values Attained					
$R^2 = 0.487$		$R^2 = 0.480$		$R^2 = 0.485$	
Model	<i>P</i>	Model	<i>P</i>	Model	<i>P</i>
Female Age	0.325	Female Age	0.351	Female Age	0.322
Year	0.038	Year	0.041	Year	0.042
Brood Size	0.002	Brood Size	0.001	Brood Size	0.001
Total Visits/h	0.459	Female Visits/h	0.620	Male Visits/h	0.492

number of young and male visits/h for the model which incorporated male visits/h as the index of parental care ($R^2 = 0.478$).

These multiple regression analyses show that although female age, year and brood size often contribute significantly to explaining the variability in the growth indices, the parental care factors (total, female or male visits/h) are only significant in one case (male visits/h for wing maximum values). These results suggest that the number of visits made to the nest is less important to the overall growth of the young when placed in context with the other explanatory factors.

Table 30. Multiple linear regression of nest mean growth variables: Wing growth constants and maximum wing values.

Dependent variable: Nest Mean Wing Growth Constant					
$R^2 = 0.352$		$R^2 = 0.431$		$R^2 = 0.390$	
Model	<i>P</i>	Model	<i>P</i>	Model	<i>P</i>
Female Age	0.021	Female Age	0.015	Female Age	0.014
Year	0.932	Year	0.713	Year	0.986
Brood Size	0.047	Brood Size	0.003	Brood Size	0.155
Total Visits/h	0.916	Female Visits/h	0.079	Male Visits/h	0.232

Dependent variable: Nest Mean Wing Maximum Values Attained					
$R^2 = 0.453$		$R^2 = 0.385$		$R^2 = 0.478$	
Model	<i>P</i>	Model	<i>P</i>	Model	<i>P</i>
Female Age	0.001	Female Age	0.003	Female Age	0.001
Year	0.446	Year	0.535	Year	0.508
Brood Size	0.016	Brood Size	0.083	Brood Size	0.010
Total Visits/h	0.072	Female Visits/h	0.485	Male Visits/h	0.038

Another approach avoiding the problems with non-independence of measurements is to test the strength of the relationship between the condition of young in the nest (brood weight or mean young weights) and parental care measures (visits/h: total, female or male) by day of observation. Day 13 represents the time when, overall, adults are exerting maximum levels of effort as evidenced by the highest of visits/h being made to the nest. Day 13 is also the time when young are reaching their maximum weights and will soon undergo a weight recession prior to fledging. Because of these factors, day 13 is likely the best of any of the five days of observation with which

to assess whether or not there are differences in abilities in providing parental care. Because growth of young was not measured on the same days that behavioral observations were obtained, weights of young on days 1, 5, 9, 13 and 17 were interpolated from data points surrounding them. For example, day 13 data were calculated as the midpoint between days 12 and 14 growth measures.

Multiple linear regression analyses of brood weights (weight of all nestlings in a nest summed) on day 13 (Table 31) show a significant effect of the number of young in the nest for all three models (R^2 range = 0.486-0.507), which is expected given the fact

Table 31. Multiple linear regression of day 13 posthatch mean growth index variables: Brood weights and nest mean nestling weights.

Dependent variable: Day 13 Brood Weights					
$R^2 = 0.486$		$R^2 = 0.501$		$R^2 = 0.507$	
Model	<i>P</i>	Model	<i>P</i>	Model	<i>P</i>
Female Age	0.214	Female Age	0.172	Female Age	0.163
Year	0.644	Year	0.854	Year	0.633
Brood Size	<0.001	Brood Size	<0.001	Brood Size	<0.001
Total Visits/h	0.819	Female Visits/h	0.347	Male Visits/h	0.270

Dependent variable: Day 13 Nest Mean Nestling Weights					
$R^2 = 0.260$		$R^2 = 0.289$		$R^2 = 0.280$	
Model	<i>P</i>	Model	<i>P</i>	Model	<i>P</i>
Female Age	0.212	Female Age	0.163	Female Age	0.171
Year	0.791	Year	0.996	Year	0.763
Brood Size	0.025	Brood Size	0.031	Brood Size	0.010
Total Visits/h	0.989	Female Visits/h	0.291	Male Visits/h	0.383

that only two brood sizes were included in the experimental design. The other factors were not significant. For mean nestling weights on day 13 (Table 31), there was also a significant effect of the number of young in the nest for all three models, yet less of the variability in the dependent variable was explained (R^2 range = 0.260-0.289). Mean nestling weights on day 13 for nests with four young were significantly higher than those for nests with six young (t-test, $t = 2.920$, $P = 0.006$), suggesting that young in smaller broods are receiving, on average, more food per trip to the nest since the parental care factor was not significantly different.

Mortality Rates of Treatment Group Young

During 1990, mortality of young occurred only in the SY with six young treatment group (Table 32). In addition, each of the four nests in this treatment group lost young: two young each from two nests, and one young each from two nests. Because there was lack of mortality in three of the four treatment groups (*i.e.* cells with zeros), I did not analyze these data using multidimensional contingency tables.

During 1993, mortality was spread among all four treatment groups and ranged from 8.3 to 42.9% (Table 32). A test of mutual independence was rejected ($\chi^2 = 11.44$, $df = 4$, $P = 0.022$), so three tests of partial independence were conducted. Two of the three tests were rejected (both $P < 0.014$). The test not rejected ($\chi^2 = 2.03$, $df = 3$, $P = 0.567$), was that female age was independent of brood size and the likelihood to fledge. Because it was not rejected, it was permissible to test the hy-

pothesis that likelihood to fledge was independent of brood size (Zar 1984, pg. 77).

This hypothesis was rejected ($\chi^2 = 10.208$, $df = 1$, $P < 0.001$), which indicates that overall fledge rate was dependent upon the number of young in the nest. During 1993, mortality rates were higher at nests with six young, regardless of the age of the female (Table 32).

Table 32. Likelihood of mortality of treatment group young, 1990 and 1993.

Year	Treatment Group	# Fledge	# not Fledge	% Fledge	% Mortality
1990	ASY/4	12	0	100.0	0.0
	ASY/6	24	0	100.0	0.0
	SY/4	12	0	100.0	0.0
	SY/6	18	6	75.0	25.0
1993	ASY/4	23	5	82.1	17.9
	ASY/6	24	18	57.1	42.9
	SY/4	22	2	91.7	8.3
	SY/6	38	16	70.4	29.6

Mortality rates reported here are from all treatment group nests which were established. Unfortunately, not all of these nests were used for growth and parental care measures because of early failure. Because of this, complete comparisons of parental care and potential impacts on mortality rates were not possible.

WEIGHT CHANGES IN PARENTS FEEDING YOUNG

The relationship between adult weights (both male and female, total $n = 102$ measurements on adults from 16 nests) and age of the young during 1990 showed that, in general, adult weights decreased through time (Table 33, all data pooled). Linear regression showed that the slope for pooled data was marginally significantly different from zero ($P = 0.050$), yet the fit was poor ($R^2 = 0.038$). Although adult weights decline from the time following hatching through the middle portion of the nestling period, weights appear to increase at the end of the nestling period.

Analyzed by treatment group (Table 33), only adults at ASY nests with four young show a slope significantly different from zero ($P = 0.017$) that corresponds to a decline in weight over time. Adults at ASY nests lost more weight over time than did adults at SY nests (slightly steeper slopes), and adults at SY nests with four young actually increased in weight slightly over time (slope = 0.016), although not

Table 33. Linear regressions of adult weights as a function of age of young during nestling rearing. All data are from 1990.

Adult Weights				
Treatment Group	n	R^2	Slope	P
ASY With 4 Young	21	0.266	-0.104	0.017
ASY With 6 Young	27	0.087	-0.077	0.136
SY With 4 Young	26	0.005	0.016	0.720
SY With 6 Young	28	0.013	-0.033	0.570
Pooled Groups	102	0.038	-0.050	0.050

significantly. Both of these observations are contrary to predictions that adults at SY would be stressed to a greater degree from the rigors of feeding young and as a result would lose more weight. In addition, during 1990, adults at ASY nests with six young showed much higher levels of parental care measures, yet, on average, lost less weight than parents at ASY nests with four young.

All regressions for treatment groups, with the exception of ASY nests with four young ($R^2 = 0.266$, $P = 0.017$), show a poor and non-significant fit to the linear model (all $R^2 < 0.087$, all $P > 0.13$), suggesting both a high degree of variability between individual adults and perhaps that a non-linear relationship would be more appropriate. Some individuals within the same treatment group gained weight, while others lost weight, suggesting some individuals are better able to maintain or even increase energy reserves while at the same time feeding young. This finding is interesting in light of the significance of the nested growth models presented earlier which suggested that much of the variability in growth can be attributed to the individual nest.

DISCUSSION

AGE CLASS DIFFERENCES: PRE-HATCHING

Clutch Size and Egg Weights

Clutch sizes were significantly smaller (Figure 2, Table 4) and were initiated significantly later (Figure 1, Table 3) for SY females throughout the study. Although there were some years when mean clutch size values were similar for the two age classes and standard error bars overlapped (*e.g.* 1987), and all of the assumptions of the test could not be met, analysis of covariance shows a strong effect of female age, even after controlling for a significant effect of initiation date (see also Perrins 1965, Stutchbury and Robertson 1988). Similar relationships between female age and clutch size in Tree Swallows have been reported previously (DeSteven 1978, Stutchbury and Robertson 1988). The significant initiation date finding is important because it has been shown in a number of species, with all else being equal, later nesters produce fewer young which survive (*e.g.* Reese and Kadlec 1985, Perrins 1970). Because the number of young banded at Panola Plains which return to breed is very low ($< 1\%$), it has not been possible to test for differential young survival rates.

Both inexperience and foraging deficiencies on the part of SY females have been thought to be important factors resulting in smaller clutches and lower reproductive

output (Lack 1968, Perrins 1970). Since food abundance impacts both clutch size (*e.g.* Hussell and Quinney 1987), and growth of young (*e.g.* Quinney *et al.* 1986) in Tree Swallows, Stutchbury and Robertson (1988) reasoned that if clutch size differences between SY and ASY females were due to foraging deficits, then these differences would likely be lessened in a food rich environment. This is a compelling and testable hypothesis, yet they provided no evidence for this. Desrochers (1992) found that clutch size in European Blackbirds overall was increased when he provided supplemental food, yet the magnitude of differences between SY and ASY females persisted. DeSteven's (1978) study was conducted at Long Point, Ontario where prey abundance, in the years following her study (measured as insect biomass indices, Hussell and Quinney 1987) was found to be much higher than at Panola Plains (Hussell *et al.* 1990). The range of differences between age classes reported by DeSteven (1978) was greater (0.8 and 0.9 eggs/nest, respectively, in a two year study) than reported in my study (0.186 eggs/nest in 1987 to 0.647 eggs/nest in 1991), yet she also reported overall larger clutch sizes for both female age classes as well. Even though there were potentially large differences in prey abundance between DeSteven's study and this study, the difference in magnitude of clutch size between SY and ASY females is in the opposite direction of that predicted by Stutchbury and Robertson (1988). Although prey abundance has been documented to have a significant proximate influence on clutch size (Hussell and Quinney 1987, Järvinen and Väisänen 1982, 1984, Perrins and McCleery 1989), it does not appear to affect the relationship between SY and ASY females.

In this study individual egg weights were also shown to be smaller for SY females, and yearly differences ranged from 0.007g/egg in 1993 to 0.094g/egg in 1992. The range of differences was similar when nest mean egg weight was considered. Egg weights in SY Tree Swallows were also shown to be significantly smaller by DeSteven (1978) with a similar range of differences. Wiggins (1990) reported marginally non-significant differences in mean egg weight between the two age classes, yet his sample sizes were much smaller than what is reported here ($n = 16$ SY female nests, 121 ASY female nests, over three years). In this study, depending upon the year, nested analysis of variance showed that between 74 and 81 % of the variability in egg weights was attributable to the nest (*i.e.* individual female) where the eggs were laid. Factors contributing to the importance of the nest include primarily attributes of the individual female, and possibly also nestbox location and time of season. Because of the significant effect due to the individual female in the nested analysis of variance, female age was a significant factor only during 1992 (Table 9, $P = 0.028$). Wiggins (1990) also found a high degree of among-clutch variability in Tree Swallows, which amounted to 79% of the total variation in egg weights. The large proportion of the variability in egg weights and measurements attributable to individual females is also reported in other species. Ojanen *et al.* (1981), in four species of passerines, also showed that approximately 50-70% of the variation in egg dimensions (weights were not reported) was attributable to the female from which they came (see also Järvinen and Väisänen 1983, Jover *et al.* 1993).

Differences in egg weights could be due to genotypic differences of females, or phenotypic adjustments due to factors such as seasonality, weather, food abundance or laying sequence (O'Connor 1979). Although it appears that the age of the female has considerable influence on the weight of eggs, this effect is difficult to discern using nested models where an individual female factor is included. There appear to be inherent differences in the abilities of individual females to produce larger eggs, and these differences have an age-related component as well.

Ricklefs (1974) argued that if a female is stressed energetically, the quality and size of eggs she produces are not altered appreciably, but only the number, whereas others have shown that poor feeding conditions at the time of egg formation can result in lower quality or smaller eggs (Martin 1987, Ojanen *et al.* 1981, Perrins 1979). Egg weights have been shown to be correlated with the overall physical condition of the female (Järvinen and Väisänen 1984, Murphy 1980, Murphy 1986), and the size and quality of eggs have been shown to increase in times of high food abundance (Bryant 1978a, Ewald and Rohwer 1982, Högstedt 1981b, Järvinen and Väisänen 1984). Egg weights in my study varied from year to year (Figure 4), and presumably these differences could be due to yearly changes in food availability. The magnitude of differences between SY and ASY egg weights has also varied across years, yet whether or not this yearly variability is due to age-related responses to food abundance is unknown.

In this study, repeatability of clutch size was lower in SY females advancing into the ASY age class when compared to ASY females encountered over two subse-

quent years. This suggests there is at least some improvement with age for SY females, and the improvement is in the direction predicted, yet comparing mean clutch sizes for this subset of females showed they were not significantly different. In addition, the improvement recorded (approximately 0.18 eggs/nest) was of a lower magnitude than the differences between age classes in an average year (approximately 0.4 eggs/nest). Similar results were reported by Smith (1993) in Marsh Tits (*Parus palustris*), where significant differences of 0.37 eggs/nest for age class comparisons were larger than the non-significant 0.14 eggs/nest for individual females aging from SY to ASY. The majority of studies investigating age-related reproduction have been cross sectional rather than longitudinal, and although studies of long-lived species have shown increases in clutch size with age (*e.g.* Coulson 1966, Hamann and Cooke 1987), relatively few studies in short-lived species have shown actual improvements in individuals as they age. Changes in mean clutch size with age can be the result of an improvement of performance in individuals, or it can be a result of differential mortality on poorer SY performers, thus shifting the mean values for the cohort upward (the selection hypothesis of Nol and Smith 1987). Högstedt (1981a) found no increase in clutch size as individuals aged in a small sample of Magpies (*Pica pica*). Similar results were reported by van Noordwijk *et al.* (1981) for a large sample of Great Tits and by Nol and Smith (1987) in Song Sparrows (*Melospiza melodia*). Desrochers and Magrath (1993), studying European Blackbirds (*Turdus merula*), did report an increase in clutch size of 0.4 egg/nest in individual females aging from one to two years, and this being in a species with a smaller clutch size than Tree Swallows (range 1-5 eggs, no mean

value presented). Desrochers and Magrath (1993) concluded that this increase in clutch size was not due to a reduction in the proportion of poor performers, but improvements in individuals over time—they found no correlation between fecundity in SY females and their probability to survive to the next year.

In contrast to clutch size repeatability, egg weight repeatability was much higher for both groups considered in the analyses (SY aging to ASY, and ASY individuals encountered over two years). In other words, eggs produced by the same female remained generally stable in weight from year to year, regardless of age class. Significant intraclass correlations indicate that the variability associated with year-to-year changes in the same individual is low compared to the variability between individual females. Even though repeatability of egg weights was high, the values were lower for SY females, suggesting that the potential for change as SY females aged was greater than for ASY females encountered over two years. This suggests there is at least some improvement with age for SY females, and the improvement is in the direction predicted, yet comparing mean egg weights for this subset of females showed they were not significantly different. The improvement recorded (approximately 0.031g/egg) was of a lower magnitude than the differences between age classes in an average year (approximately 0.041g/egg).

Hatching Success, Egg and Nest Failure

In this study, SY females showed a greater likelihood of egg loss over time than ASY females. This is evidenced by both a lower rate of hatching (Table 10) and higher mortality rate of eggs in the nest (Table 11). Lower egg hatching rates by SY females in my study are contrary to DeSteven's (1978) findings where the hatching rate of eggs from SY female Tree Swallows was slightly higher than eggs from ASY females. DeSteven reported only two years of data, and although mean hatching rates were higher for SY females, they were significantly higher only in one of two years when analyzed separately. An overall lower rate of hatching was also observed in SY females by Brown (1978) in Purple Martins (*Progne subis*), as well as other species (Aldrich and Raveling 1983, Boekelheide and Ainley 1989, Røskoft *et al.* 1983). Many studies, however, show no differences in hatch rate due to age (Hannon and Smith 1984, Nol and Smith 1987, Perrins and Moss 1974, Rockwell *et al.* 1993, Sæther 1990). The lower rates of hatching by SY females reported in this study may be due to poorer quality incubation behavior, higher rates of infertility, or a higher rate of developmental abnormalities resulting in embryo death. A lack of constancy in egg temperature maintained during incubation can lead to developmental abnormalities and influence hatching success (Drent 1975). Aldrich and Raveling (1983) showed that younger Canada Geese were less attentive incubators and this was correlated with lower hatching success. Older females started incubation in better body condition than younger females and thus were able to spend less time foraging which resulted in more time

sitting on the eggs. In my study, SY females produced smaller eggs, and hatching success is also generally thought to be related to egg size (Martin 1987). Rofstad and Sandvik (1985) reported that smaller eggs in the Hooded Crow (*Corvus corone*) were less likely to hatch. Järvinen and Väisänen (1983) showed that hatching success in the Pied Flycatcher (*Ficedula hypoleuca*) at the northern end of the species' range was related to egg size and that larger eggs hatched with greater frequency. They suggested that larger eggs could better withstand cooling conditions when the female left the nest to forage because of their larger thermal mass. In my study, SY females only produced approximately 90% of ASY clutch biomass. It is not clear whether or not differences of this magnitude would produce differences in thermal mass great enough to influence foraging dynamics and the time spent off the nest during incubation.

The higher rate of egg mortality observed could be due to inherently higher predation rates on eggs in SY nests, which may be related to nestbox location. Nest site location has been shown to influence several breeding variables in other species, such as nest initiation date, clutch size and nest failure rate (Högestedt 1980, Middleton 1979, Nilsson 1984, Perrins and Moss 1975), and younger females have been shown to have a higher likelihood of settling in marginal habitats in Black-billed Magpies (*Pica pica*) (Reese and Kadlec 1985). It appears that the dispersion of SY nests at Panola Plains was not random, but was clumped, and SY females were more likely to nest in areas of the plot characterized by higher density of shrubs, or on the edge of the nestbox arrays which are often adjacent to forest edge. Tree Swallows prefer open habitats, and, if

possible, avoid brushy areas and forest edge (Rendell and Robertson 1990). These brushier areas of the plot are ideal House Wren (*Troglodytes aedon*) habitat, and interference competition by wrens (Finch 1990, Rendell and Robertson 1990) for nesting sites may partially explain the higher egg losses in SY females. House Wrens will enter nestboxes of other species and poke holes in eggs, remove eggs entirely from the nestbox, and in some cases, kill young (Belles-Isles and Picman 1986, Kendeigh 1941). Although I did note wren predation when it was obvious, I do not have detailed enough information to test this interference hypothesis. Wren interference often results in nestbox takeover (personal observation), and total nest failure was significantly higher for SY females during two of eight years of the study (Table 12) compared to ASY females. These same two years (1989, 1992) were also characterized by episodes of cold and wet weather during the nestling phase which had a significant impact on young in the nest (Beaver *et al.* 1994). During these periods of inclement weather, adults abandon the nest, leaving the young to die from exposure. Late nesters which were still incubating are also impacted and may also abandon nests. Since SY females initiate nests significantly later, this may partially explain their higher rate of nest failure in those years.

Another factor correlated with increased likelihood of nest abandonment during incubation reported in the literature is egg size. Smith *et al.* (1993) found that higher rates of nest abandonment in European Starlings occurred at nests with smaller eggs.

These results are only correlational, yet are interesting in view of my results where SY females produced smaller eggs and also showed higher rates of nest failure.

THE ENERGETICS OF EGG PRODUCTION AND INCUBATION

In terms of clutch biomass, SY females, over the entire study, produced on average 0.912 g/nest less than ASY females, or approximately 90% of ASY output. Walsberg (1983) calculated that for five small passerines, the energetic content of the clutch is only approximately 2% of the female's total energy expenditure during a single reproductive event. So, although differences in clutch size and egg weight between SY and ASY female Tree Swallows are statistically significant, they appear initially to be very small in light of a female's total energy output for the breeding attempt. However, energy for egg formation is not the only expenditure needed for successful egg production and hatching, as there are many other related costs. Although the male helps defend the nestbox and provides the nest lining consisting of feathers he has collected, nest building, egg laying and incubation behaviors in Tree Swallows are exclusively female (Turner and Rose 1989). Female Tree Swallows, like most passerines, are "daily surplus" users of energy during egg formation (Perrins and Birkhead 1983), that is, they increase intake of daily energy in order to produce eggs. There are no reports of male Tree Swallows feeding their mates during this time, so energetically speaking, the female is entirely responsible for the formation of eggs. She must take in enough energy for maintenance, plus additional energy for egg formation and produc-

tion of one egg per day for two to seven days, depending on the size of her clutch. In addition, there is the cost in energy prior to egg formation required for gonadal development. Once the clutch is complete, the female must then keep the eggs warm for approximately 14 days during the incubation period. The incubation period is likely the least energy demanding phase of breeding (King 1974, Walsberg 1983, Williams 1988), yet the male Tree Swallow does not feed the female during this time, so she must leave the nest to forage in order to maintain her energy balance. Even in species where males feed the incubating female, weight loss by females during incubation has been reported (van Balen 1973). Rewarming of eggs upon returning from foraging in single sex incubators (*e.g.* Tree Swallows) is energetically expensive, as it has been shown that metabolic rate increases up to three times when cold eggs are rewarmed in the European Starling (Biebach 1979). Westerterp and Bryant (1984) also found in a comparative study of aerial insectivores that incubation is more energetically expensive in a single-sex incubator compared to species which share incubation duties.

Although egg formation and incubation can be energetically expensive when viewed in a broader context than simply laying and then sitting on eggs, in terms of age-related effects, there is little information available. However, if SY females were indeed deficient in foraging abilities, or, perhaps more importantly, deficient in the overall management of time and energy, one would expect them also to be less effective incubators and this could result in fewer eggs hatched or a higher likelihood of nest abandonment.

AGE CLASS DIFFERENCES: POST-HATCHING

Male versus Female Contributions

In species that exhibit biparental care, it is thought that male parental care contributions to the young are made in inverse proportion to the abilities of females to successfully fledge young without male assistance (Clutton-Brock 1991, Emlen and Oring 1977, Orians 1969b), and that geographical areas with greater resource availability will be characterized by lower levels of parental care by males. Dunn and Robertson (1992) reported that male parental care in Tree Swallows was more important to overall nesting success in areas of comparatively lower food abundance, which supported this view, yet how this is related to SY females' abilities to provide parental care and the assistance they receive from male partners is unknown. In areas of high insect abundance, Tree Swallows, which are normally monogamous, may exhibit a low incidence of polygyny (5-8% of males, Dunn and Hannon 1992, Dunn and Robertson 1992, Quinney 1983). Because of this, some females may go without any male assistance in feeding young, since males rarely contribute at secondary nests (Dunn and Hannon 1992). Available insect biomass was much lower at Panola Plains (D. Hussell, personal communication, Hussell *et al.* 1990) when compared to the Ontario and Alberta sites used by Dunn and Robertson (1992). In my population of Tree Swallows, few differences were shown in the frequency of visits to individual nests when males and females were compared, and within treatment groups, the frequencies of male and female visits were significantly correlated. The importance of biparental care in the

Panola Plains population is emphasized by the observation that in all cases where a nest appeared to have only one adult parent actively feeding young, the nest failed. There are reports of single parents successfully fledging young in areas characterized by high insect abundance (Dunn and Hannon 1992, Quinney 1986). If SY females were less able to raise young because of deficiencies in their abilities to provide parental care, it is expected there would be differences in the proportion of male and female contributions at SY and ASY nests, yet this was not observed in this study. Equal provisioning could be the case if SY females were more likely to mate with SY males that were also deficient in breeding capabilities, yet I do not have any evidence for assortative mating according to age. Most often, I was not able to determine the age of the male other than a minimum known age, yet there was no difference in the likelihood that an SY female would mate with an unbanded male (potentially an SY male) or a previously banded male (a certain ASY male, unless banded as a young in the nest) when compared to ASY females ($n = 74$ pairs, $\chi^2 = 1.66$, $df = 1$, $P > 0.1$). While some studies have shown assortative mating with respect to age (Bryant 1979, Crawford 1980, Lessells and Krebs 1989, Smith 1993), others have not (Harvey *et al.* 1985, Perrins and McCleery 1985). Furthermore, Quinney (1986) and Leffelaar and Roberston (1986) also found that male and female visits by Tree Swallows to the nest were approximately equal, whereas Lombardo (1991) did find some significant differences, although all of these studies measured and analyzed parental care data somewhat differently. In the present study, of the four nests in 1990 which showed significant differences in the proportion of male and female visits, two were SY nests with six young

(both of which had significantly higher levels of female visits, which incidentally is contrary to predictions), one was an SY nest with four young (higher male visits), and one was an ASY nest with four young (higher male visits).

Enoksson (1993) reported in European nuthatches (*Sitta europaea*) that the male's age had no effect on any of the reproductive variables measured in his study. Other studies have found that the male's age was a significant factor contributing to the fledging of young, yet had no effect on the clutch size produced by the female. Hannon and Smith (1984), for example, showed in Willow Ptarmigan (*Lagopus lagopus*) that pairs of two adults (versus some combination including a subadult) fledged the most young, yet male age did not influence clutch size or laying date of the female. Perrins and McCleery (1985), in Great Tits, also found that the age of the male significantly affected fledge rate, yet had no influence on female clutch size (see also Reese and Kadlec 1985). Female European Blackbirds did not adjust clutch sizes based on the age of the male, even though older males provided higher quality parental care, as it was shown that they were more proficient foragers than younger males (Desrochers 1992, Desrochers and Magrath 1993). It may be the case in many species that females are not able to assess the quality of their mates prior to the time when males and females begin sharing of parental care duties by feeding young (*e.g.* Desrochers and Magrath 1993, Slagsvold and Lifjeld 1988, 1990), unless they had previously mated.

Overall Parental Care

Williams (1988) found a positive association in Tree Swallows between the number of visits made to the nest and metabolic rates measured using the doubly labeled water method. Greater rates of visitation resulted in higher rates of energy expended, and he suggested that nest visitation rates were a reasonable measure of parental effort (see also Bryant and Tatner 1990). Bryant and Westerterp (1983) found no significant differences in average daily metabolic rates that could be attributable to female age during the time of feeding nestlings. Even though no differences were found, the amount of energy collected for delivery to young in the nest per unit of energy expended could be vastly different depending on potential differences in foraging efficiency (Bryant 1982). Because of potential differences in load sizes of food delivered to young which vary according to year, age of young, individual nest, and to a lesser degree, the sex of the adult parent (see below), inferences drawn from the number of visits made to the nest as they relate to the overall growth of the young will be much more conclusive if these factors can be taken into consideration (Royama 1966).

Graphically, there appear to be differences in parental care associated with treatment groups and years (Figures 6 through 9), yet repeated measures analysis of variance on total visits/h did not detect any significant effects due to female age (nest type) or year. The response variables female visits/h and male visits/h gave the same results. Only brood size had significant effects on nest visitation rates in all three of

these models. At nests with four young, a consistent pattern of total, male and female visits/h was detected, with no effects due to age of the female or year, so it appears that the level of parental care is very uniform at these nests, including across years which may differ in extrinsic factors such as food abundance and weather conditions. The pattern at nests with six young, however, was much different, with a significant female age $\times$ year interaction for total, male and female visits/h models. This indicates a variable response between the two years under study for nests with SY vs. ASY females and this is apparent in Figures 6 and 8. The prediction that adults at SY nests would provide lower levels of parental care appears to be partially supported during 1990 at nests with six young when adults at SY nests provided parental care at only approximately four-young levels. During 1993, however, the prediction is not supported, and the response is actually in the opposite direction of that predicted; adults at SY nests provided a higher level of parental care when compared to ASY nests which were now visiting at approximately four-young levels.

The uniform response in terms of visits/h at nests with four young (with no year effect) indicates that parents generally do not differ in their abilities to provide care at the levels necessary for this brood size. With brood sizes of six young, however, the variability in response between treatment groups increases, indicating that the increased burden of feeding greater numbers of young may be taxing the abilities of some adult pairs to provide adequate parental care. Interestingly, however, this apparent inade-

quacy of response switches from SY nests with six young in 1990 to ASY nests with six young in 1993.

Growth of Young

Graphically, the growth curves in 1990 appear to indicate effects due to both age of female and number of young in the nest, and the observed responses are in the direction predicted (Figures 11 and 12). As predicted, ASY nests with four young show the best growth over the observation period (for both weight gain and wing length increase), whereas SY nests with six young show the poorest. The young at the two remaining treatment groups (ASY nests with six young and SY nests with four young) show intermediate values, and appear to grow at approximately the same rates. These results are similar to those of DeSteven (1978), who showed that fledging weights of young were negatively affected by brood enlargement at SY nests, but not at ASY nests. During 1993 (Figures 13 and 14), however, the same relationship does not hold, particularly for wing growth where little, if any, differences are shown between treatment groups. For the variable of weight there is some separation between treatment groups, yet the separation is slight and relationships between treatment groups (best to poorest) are different than those observed during 1990.

The non-nested analysis of variance models on growth variables reveal some significant main effects (with the exception of weight growth constants), yet the interpretation of these results is severely confounded by significant interaction terms (Sokal

and Rohlf 1981) which are also frequently present in the models. For example, results of analysis of variance on wing growth constants (Table 25) show that three of the four interaction terms are significant. Even though there is a significant effect due to female age, the female age factor also interacts with year alone, and year and brood size in combination. These significant interactions suggest that although there are statistically significant differences between treatment groups for the growth variables measured, these differences are not consistent across levels of factors used in the models. Significant second order interactions make interpretation particularly difficult, yet do indicate highly variable growth patterns across years and nest types.

Nested analysis of variance reveals that growth of young in all four treatment groups was much more heavily influenced by the factor of nest than by female age, year, or number of young in the nest, and this was true of all the growth variables reported, especially the fitted growth constants for weight, where only 3.5% of the variability could be attributable to factors other than the nest. Growth of individual young has been shown to be highly dependent upon the nest in which they are raised (DeSteven 1980, Quinney *et al.* 1986). This study is in agreement since variability in the growth patterns observed was much more strongly influenced by the individual nest than treatment groups characterized by the age of the female and brood size. Because the factor of the nest is significant for all of the dependent growth variables tested, this result suggests that individual adult pairs feeding the young may be performing quite differently when compared to one another. Regardless of the age of the female or year,

adult pairs are likely delivering food at different rates, or in different quantities at the same rate of visitation (Royama 1966), and highly variable growth patterns result. O'Connor (1975) concluded that the young of aerial insectivores exhibited highly variable growth patterns due to the unpredictable patterns of food availability is determined primarily by prevailing weather conditions (see also Bryant 1978a, Jones 1987c, Turner 1983). The unpredictability of food resources results in the number of visits made to the nest and the amount of food delivered to the young to be highly variable (Bryant 1978a). Studies on other aerial insectivores have drawn similar conclusions; growth of young is closely associated with the amount of food available to the adults (Bryant 1975, 1978b, Quinney *et al.* 1986). Depending upon the time frame, some nests can be impacted by inclement weather and the associated decrease in insect abundance much more than other nests, and this can be reflected in the overall growth of young. With these relationships in mind, the data presented here suggest that the observed patterns of growth potentially result from differences in pairs' abilities to capitalize on fluctuating resources.

Relationship Between Parental Care and Growth of Young

Ricklefs (1977) makes the point that, evolutionarily speaking, parental care, feeding of the young, and growth of young are interrelated and optimized as a unit. Because the growth of young is a direct result of the quantity and/or quality of parental care, the relationship between these factors is the key to understanding whether or not

the ability to provide parental care is a possible determinant of clutch size in younger females.

During 1990, adults at SY nests with six young made visits to the nest at a rate approximately 80% of the other three treatment groups (Figure 19), and this is reflected in the poorer growth of young in this treatment group (Figure 11). The 1990 growth data and parental care data, when considered as separate results, support the hypothesis that adults at SY nests provided a lower level of parental care and that young grew more poorly as a result. Viewed within the context of all treatment groups, however, there is a lack of correspondence between parental care and growth measures; high rates of visitation did not always translate into better overall levels of growth. Even though SY nests with six young showed the poorest growth and lowest per young visitation rates, the lack of correspondence between parental care and growth in the other treatment groups weakens the conclusions. Support for the major hypothesis that SY females are constrained by their inability to provide parental care would be much stronger for the 1990 data if all treatment groups responded as predicted.

During 1993, the lowest levels of visits/young/h were measured at ASY nests with six young and performance was approximately 80% of that observed for means from the other three treatment groups (Figure 19). Growth curves also showed that ASY nests with six young had the poorest weight gain as well (Figure 13), yet the curves were not clearly separated, and this is particularly evident for wing growth

(Figure 14). This is in contrast to 1990 data when SY nests with six young clearly showed the lowest levels of parent visitation and the poorest growth curve.

Correspondence between visitation rates and growth measures during 1993 do not support the prediction that adults at SY nests would provide lower quality parental care resulting in poorer growth of young. The correspondence between visitation rates and growth measures within treatment groups is better during 1993 than that observed during 1990, yet still there is a marked lack of consistency; high rates of visitation did not always translate into better overall levels of growth. This is underscored by the results of multiple regression analyses on growth variables which showed that indices of parental care rarely explained significant proportions of the variability, whereas the other independent variables of nest type (SY or ASY), year and brood size often did. This suggests that factors other than the number of visits *per se* made to the nest are more important contributors to the growth patterns of young observed in this study.

Even though there were generally no differences in proportions of male and female visits, the quality of the visits themselves may be highly variable. Across two years of observations (1990 and 1993), the proportion of male and female visits to the nest did not differ to any appreciable degree. However, when boluses were collected during 1991 (unfortunately, sample sizes were small and only collected during late or renesting), I found that males delivered significantly larger boluses to the young (after controlling for age of young using analysis of covariance), which essentially can be translated into higher quality parental care for the same quantity of visits to the nest.

The measures of bolus weights for males did not change over time (slopes did not differ significantly from zero), yet bolus weights did increase for females. Females increased load sizes as the young aged, yet the males did not. This could be attributable to a tendency of males not to increase parental investment as the young aged, similar to that which was observed in Great Tits (Slagsvold and Lifjeld 1990). Jones (1988) also reported that males were more likely to engage in self feeding during times of low prey abundance, whereas females were more likely to feed young and lost more weight as a result. Boluses were also collected during 1989 and 1990, and when the years are analyzed together, it was found that mean bolus weight (once again taking age of young into account using analysis of covariance) was significantly different between years. This is not likely attributable to different collection times since these were all late season nests, and all years showed significant increases in bolus weight as the young aged. More likely the cause is differences in prey abundance between years, and this can have a profound effect on how hard the adults have to work in order to keep up with the demands of the young in the nest. During times of low prey abundance adults most likely have to work harder to maintain the number of visits/h and to maintain the amount delivered per bolus. Another factor contributing to these yearly differences is the fact that during 1990 and, in particular 1989, some boluses were collected as groups which effectively reduces the variance and thus makes yearly differences more likely.

I did not measure load size delivered by males and females at the treatment nests that I was observing the number of visits at during 1990 and 1993, primarily because of the invasiveness of the ligature technique used to determine load sizes (Johnson *et al.* 1980). Results of other studies on aerial insectivores have revealed highly variable relationships between load sizes delivered and age of young and sex of adults (*e.g.* Jones 1987b, 1988, Martins and Wright 1993). Nests from late in the season in this study showed clearly that bolus size increased with the age of the young, and this trend was significant in all three years. Others have also shown a positive relationship between bolus size and age of the young (*e.g.* Johnson and Best 1982, Knapton 1984, Walsh 1978), yet Turner (1983) found that bolus size did not vary with age of the young between 7 and 18 days (Swallows, *Hirundo rustica*, and Sand Martins, *Riparia riparia*), and similar findings were reported by Jones (1987b, also in *H. rustica*). Significant differences were found in 1991 (not measured in the other two years) between male and female load size after controlling for the age of young using analysis of covariance. Females delivered loads approximately 80% of male size. These differences could be due to body size differences as male Tree Swallows are significantly larger in both weight and wing length. These findings are contrary to the study by Jones (1987b) who found, with a much larger sample size, that males, which were also significantly larger in body size, delivered significantly smaller load sizes. Another important finding was that of significant differences in average load size between years, suggesting that either prey abundance or frequency of prey sizes taken by adults differed between years. In addition, much of the variability in bolus weight from all three

years was due to day-to-day changes in load size (significant days posthatch covariate) and this variability obscured any differences due to nest type (SY or ASY nest). It appears that the lack of correspondence between the number of visits to the nest and the growth of young may be partially due to differences in load sizes delivered on each visit. A much more detailed study would be needed to assess this fully.

Mortality of Treatment Group Young

Overall mortality rates across treatment groups during 1993 were 27.7% while during 1990 were only 8.3%. In addition, mortality of young during 1993 was spread across all treatment groups, whereas during 1990 only SY nests with six young were impacted. However, even though mortality was recorded in all treatment groups during 1993, nests with six young were much more severely impacted, regardless of the age of the female. While nests with six young suffered 35.4% mortality of young, nests with four young suffered only 13.5% mortality. Turner (1983) also found that larger broods were more severely impacted by inclement weather, primarily due to larger disparities in weight of young within a brood, apparently putting some young at greater risk during times of food deprivation. Inclement weather was a major factor on mortality rates during 1993, since most mortality occurred following cold and wet weather on 16 and 19 June. As mentioned earlier, some of the nests that were included in the mortality values were not included in the parental care analyses simply because not enough observational data was collected on some of the nests.

Do Adults Undergo Increased Stress While Feeding Young?

Although sample size was small and restricted to only one year, it does not appear that adults in this study lost weight over time to any appreciable degree during the time of feeding young. Collectively, Tree Swallow adult weights appear to decline during the early portion of the nestling phase and then increase toward the end, yet the data are highly variable. Similar results were reported for Swifts (*Apus apus*) (Martins and Wright 1993) and European Starlings (Ricklefs and Hussell 1984). Jones (1987c) also found that the greatest amount of weight loss occurred prior to and during the early phase of feeding young, weights then leveled off through the remainder of the nestling period. Jones (1988) also found that adults were heavier during times of high prey abundance, and large changes in weight could occur in a matter of only several hours (see also Bryant 1979). This seems to be a general rule in aerial insectivores, and caution must be used when comparing weight dynamics of adults over time unless a specific time frame is used and can be somehow controlled for in each individual. This was not possible in my study. Some individuals may be impacted to a greater degree than others by events such as inclement weather, and their respective weight changes may reflect this. The data set presented here suggests that changes in weight are related to the age of the young, yet the data set is too small to adequately test the hypothesis that adults at SY nests, and particularly those with six young, would lose a greater amount of weight. When compared to other treatment groups, only adults at ASY nests with four young showed a linear decline in weight that was significantly different from zero, which is contrary to both the predictions in this study, and the results of Martins

and Wright (1993), who showed that with increased brood sizes adults lost a greater amount of weight. More detailed comparisons of weight changes over time in relation to female age would require a much larger sample size than what is reported in this study.

CONCLUSIONS

Prior to the hatching of eggs, when adults begin a vastly different phase of providing parental care, it is clear that SY females are deficient in several aspects of reproductive biology when compared to older ASY females. Clutch sizes and egg weights were smaller for SY females, which were shown to produce approximately 90% of ASY clutch biomass. Rates of egg loss and nest failure were also higher for SY females, and hatch rates were lower, so compared to ASY females, potential reproductive output is already lower for SY females prior to the time that nestlings need to be cared for. These results contribute to the large body of evidence which circumstantially supports the constraint hypothesis. This type of evidence, however, does not provide further insight into the mechanisms of clutch size determination and any potential influence of female age. Because there are many factors which influence reproductive success (including age), it is extremely difficult to separate the ultimate causes of clutch size determination from proximate constraints (Slagsvold and Lifjeld 1988).

In some populations, a large number of SY females never have the opportunity to breed (Brown 1969, Smith 1978, Stutchbury and Robertson 1985). Due to the fact that so many do not breed, the real differences between SY and ASY females are potentially much larger than those reported here and elsewhere. It seems clear that it would be advantageous to breed if at all possible. For example, Gustafsson and Pärt

(1990) report that lifetime reproductive success in the short-lived Collared Flycatcher (*Ficedula albicollis*) is higher for those individuals that breed in their first year of life compared to those that wait. In Tree Swallows, if SY females do not breed, it is estimated that a female must produce an average-sized brood for the following three years in order to replace herself, yet the average life span is only 2.7 years (Butler 1988). Given these results, clearly there are advantages to breeding as SY's, even at a reduced rate of production. These advantages to early breeding would be offset only if inordinately high mortality rates resulted following breeding as an SY, or if the possibility of producing surviving young was extremely low compared to the population mean. The importance of clutch-size-dependent adult mortality has been debated in the literature (*e.g.* Alerstam and Högstedt 1984), yet the impact in relation to female age has not been investigated directly. There are hints that SY females may have higher mortality rates than older females (see Lombardo 1986), yet there have been no comparisons of mortality rates of breeding versus non-breeding SY females. This would be extremely difficult to test given the fact that individuals who do not breed are rarely captured and banded: a necessary event in order to follow an individual over time.

The potential for improvement of clutch size and egg weight with age was somewhat greater for SY females (*i.e.* lower repeatability), yet the magnitude of improvement was less than the yearly differences observed between age classes. Because of the high mortality rates of adults (> 50%), it is difficult to determine whether or not

improvement is truly age-related or is due to differential mortality on the part of poorer performing SY females.

Following hatching, the entire age-related aspect of the study changes since males are now involved to a much greater degree by providing direct parental care to the young in the form of food deliveries. In general, efforts by male parents in this study did not differ significantly from that of the female. In most cases the numbers of visits made to the nest by females and males were highly correlated.

The data from 1990 seem to support the hypothesis that adults at SY nests were unable to provide adequate levels of parental care at nests with six young, when compared to ASY nests, and this was reflected in the poorer growth of those young. Moreover, the only mortality of treatment group young during 1990 occurred at SY nests with six young. In addition, the mortality that did occur took place in all four of the SY nests with six young. Two nests lost two young each, and the other two nests lost one young each. These results also support the predictions that adults at SY nests would provide lower quality or quantity of parental care. It appears that in 1990 adults at ASY nests were better able to cope with the rigors of providing care to a larger brood of six young. During 1993, results were much different than those observed during 1990. The largest discrepancy was that SY nests with six young did very well during 1993—better than ASY nests with six young, which did the most poorly of all the treatment groups. As such, the data from 1993 do not support the hypothesis that SY nests would fare more poorly, and, in fact, the opposite is true. Results from 1993

are distinct in other aspects as well. Although clutch sizes were significantly smaller for SY females, egg weights were not, as means were nearly identical in 1993. Hatching success was also significantly higher for SY females when compared to ASY females; 1993 being the only year where this occurred. Numbers of nesting SY females during 1993 were also the lowest reported in the study. Nest failure during 1992 approached 100% and was geographically widespread (Beaver *et al.* 1994), and this presumably resulted in very low recruitment into the 1993 breeding population, hence the low numbers of SY females. It may be that the characteristics that facilitated survival of fledging females from the 1992 cohort also contributed to the unusual reproductive variables measured in 1993. In other words, the females that survived to breed as SY's in 1993 may have possessed attributes which contributed to enhanced reproductive success.

During both 1990 and 1993, the correspondence within treatment groups between levels of parental care and growth of young observed was not one-to-one. That is, higher rates of visitation did not always translate into better growth. This could be attributable to differences in bolus weight delivered per visit, underscored by the fact that a significant portion of the variation in bolus weight can be accounted for by the nest itself. In other words, lower nest visitation rates could potentially provide more than adequate parental care, if weight delivered/visit was large enough. It appears that the size of the bolus delivered, as well as the frequency of visits made to the nest, is a

highly variable and highly individualized phenomenon, and these relationships, in turn, contribute to the high degree of variability in the growth of the young.

Even though there are numerous references of foraging deficiencies in juveniles and younger adults (Burger 1980 and 1990, Dunn 1972, Groves 1978, Orians 1969a, Recher and Recher 1969, Wunderle 1991), to my knowledge there is no evidence in the literature concerning such age-related foraging deficiencies in aerial insectivores or specifically Tree Swallows. In this study, no differences were found in bolus weight delivered to young between SY and ASY nests, yet the trend (although not statistically significant) was for SY females to deliver smaller loads than ASY females. Interestingly, in addition to SY females only producing 90% of ASY clutch biomass, mean bolus size for SY females was approximately 85 % of ASY bolus size. Desrochers (1992) argued that low foraging success may be a general constraint causing the age effects seen in so many avian species. This may also be the case in Tree Swallows, judging from the trend for SY females to deliver smaller loads to young in the nest. Foraging skills can improve over time (Desrochers 1992), yet if females were deficient foragers during the time of egg formation, laying and incubation, it seems unlikely that improvements within individuals of the scope needed to adequately care for young could occur over the course of only approximately three weeks time while feeding young. Marchetti and Price (1989) review age-related differences in foraging efficiency and one of the points they raise is experiential constraints. For example, some foraging techniques require a great deal of learning which involves interaction with the appro-

appropriate environmental stimuli. Whereas many fledglings undergo a period of “training” by adults, particularly in precocial species (*e.g.* Hannon and Smith 1984), there is little evidence for post-fledging care in Tree Swallows, and fledglings are completely on their own upon leaving the nest (yet see comments by Wheelwright *et al.* 1991). Even if SY females can adequately feed themselves because of the nearly year-long experience of foraging on their own, the environmental stimulus represented by young in the nest is unique, as well as very demanding, in terms of time and energy allocation. Experiential constraints could explain some of the apparent deficiencies observed (for example in the 1990 growth and parental care data), and may also help explain the ultimate reasons for clutch size differences between SY and ASY females.

The argument that smaller clutch sizes in SY females are a result of inexperience and foraging deficiencies and that these factors contribute to an overall inability to provide adequately for themselves or their young is pervasive in the literature (*e.g.* Lack 1968, Perrins 1970). One of the reasons this hypothesis is popular is due to its intuitive appeal; however, there is little but circumstantial evidence to support it. In this study, nestlings of SY females sometimes exhibited poorer growth, lower levels of parental care, and sometimes higher levels of mortality. In addition, there is some evidence that SY females deliver smaller sized boluses to nestlings. Overall, however, the evidence is inconsistent and sometimes contrary, and as such, is not strong enough to contend that SY females are constrained from producing larger clutches by their inability to feed nestlings.

The evidence reported in this study from growth analyses and patterns of parental care does not support Lack's contention that clutch size is determined by the parent's collective abilities to feed young, yet does not exclude the possibility of female control over clutch size based on her own abilities (*e.g.* Slagsvold and Lifjeld 1990). In species like Tree Swallows where both parents feed nestlings, but only the female builds the nest and produces the eggs, clutch size differences are likely determined by factors prior to laying or during incubation, as opposed to factors operating during the nestling period.

Suggestions for Future Research

As is the case with many field investigations, this study raises many new questions which it would be fruitful to pursue further. The question of whether or not Tree Swallow SY females are deficient foragers has not been addressed adequately. Although Williams (1988) suggests that the number of trips is a good reflection of parental effort, the combination of visits and amount delivered is an approach which would provide the most useful information (as originally suggested by Royama 1966). A rigorous sampling scheme using the ligature method and the blinds developed in this study would provide useful information in this regard. This was attempted during 1992 following the preliminary study of 1991 reported above, yet inclement weather prevented the gathering of any useful data. All of the nests set up for study failed.

This design would allow determination of whether or not SY females and males paired with SY females are indeed deficient foragers and whether or not partners compensate for each other's deficiencies. Another option would be to use an accurate balance system located under the nest to determine load sizes, as well as parental weight dynamics (*e.g.* Jones 1987a, b, c, 1988). In either case, a design that uses fixed brood sizes as was done in this study would be useful to assess potential differences associated with brood size as well. The difficulty with this scenario in Tree Swallows is that the percentage of SY females in the population does not lend itself well to a study of this nature and sample sizes could be restricted.

Interestingly, the bolus weight changes measured in this study over time were reflected in females but not in the males. It would be very interesting to see if this changes with a larger sample size or if the relationship remains the same. These sexual differences indicate that although the number of visits may not be different between the sexes, as evidenced by this and other studies, the amount of food delivered may be considerably different, particularly later in the nestling stage when young are largest.

There is a need to assess mortality rates of the age classes of females more closely to see if it is possible to test the selection hypothesis of Nol and Smith (1987). Some suggest higher rates of mortality in the SY age class, yet this needs to be tested further. This has not been possible in the present study because so many of the SY female nests were manipulated. This would require a long-term study, and longitudinal

studies of this nature have been attempted on short-lived passerines, yet definitive results have been difficult to obtain.

Desrochers and Magrath (1993) make a strong point that ignoring the potential age effect of mates (as was done, for the most part, in this study) could lead to spurious conclusions, especially if the effects of the sexes are in opposite directions. Future work should address this in species where there is biparental care. Because Tree Swallows are single-sex incubators, only females would exhibit egg-formation, egg-laying and incubation constraints, yet because both sexes feed the young in the nest, potential constraints impacting nestling rearing could influence both sexes. In other words, there may well be conflicting selection pressures acting upon each of the sexes. In addition, much of the available evidence in my study points to factors acting outside of the nestling rearing phase which are constraints to larger clutches in SY females.

Stutchbury and Robertson (1988) suggest that age-related differences would be less in a food rich environment. For example, Dunn (1972) reported differences between young and older birds in foraging abilities, yet these differences disappeared when prey abundance was artificially increased as a result of human activities. Although comparisons between my study and DeSteven's (1978) study have suggested otherwise, this could be tested at sites which differed in prey abundance, similar to Hussell and Quinney's (1987) work on clutch size and prey abundance. They compared clutch size output at two sites which differed primarily in the levels of insect biomass available, yet also reported that few, if any, SY females nested at the high prey abundance site. This potential problem could be eliminated by establishing nestboxes on

sites after relative prey abundance was measured in previous years. Newly established nestbox plots have been shown to attract larger numbers of SY females. Because of egg size differences observed in this study, it would be interesting to see if these differences were also correlated with gonad size as was suggested by Westin (1989, cited in Enoksson 1993). This would necessarily be an invasive study, yet might provide one of the more definitive pieces of information concerning the possibility of physiological or morphological constraints on egg size.

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