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Abstract

We extensively monitored the nests of Tree Swallows *(Tachycineta bicolor)* at 100 nest boxes every day during each breeding season from 1992 to 2006. The birds were banded and recorded as a means to track those who returned as recruits. We identified 166 recruits; the sex ratio of recruits was not significantly different from 50:50 and the distribution of recruits between nests was no different than expected by chance. We calculated a local recruitment rate of 4.79% when considering all nestlings (N=3463). We found a significant difference between brood size at hatching categories (1-3, 4, 5, 6, 7-8) and whether or not a recruit was produced ($p<0.05$). But this difference disappeared when limiting consideration to the most common brood sizes of 4, 5, and 6. Therefore the likelihood of producing a recruit is not influenced by family size across the most common brood sizes. We found a significant relationship between clutch initiation date and whether or not a recruit was produced for all nests ($p<0.05$). We suggest this to be an example of the "relative age effect." We also found clutch size was negatively correlated with clutch initiation date ($p=0.00$). We found no significant effects of the mother's age or physical characteristics of the parents on the likelihood of producing a recruit.

Introduction

Philopatry is important to the reproductive success of Tree Swallows *(Tachycineta bicolor)* because it provides individuals experience and knowledge about the local breeding area. Combined local experience in breeding pairs of Tree Swallows has been shown to significantly affect clutch initiation date (Lombardo & Thorpe, 2010). Clutch initiation date is important to the reproductive success of Tree Swallows; as clutch initiation date increases, clutch size decreases (Shutler et al., 2006). Philopatry is beneficial to Tree Swallows because returning to their previous breeding site allows them to acquire nest cavities earlier and subsequently begin breeding earlier in the season (Lombardo & Thorpe, 2010). Therefore local experience is advantageous to Tree Swallows because the likelihood their young will recruit is greatest for nestlings hatched earliest in the season (Lombardo & Thorpe, 2010). Experienced breeders possess information about the local area allowing them to "fine-tune" their nest site selection based on actual breeding experience as opposed to those that are immigrating from other territories (Winkler et al., 2004).

Migratory songbirds display a striking degree of philopatry; approximately 50% of breeding adults return to the same site to breed each year (Greenwood, 1980). Once they have begun breeding at a site, Tree Swallows are highly philopatric (Winkler et al., 2004). However, in the present study we are investigating the dispersal or recruitment of Tree Swallows prior to their first breeding attempt. In Tree Swallows, individuals that fail to return to their natal site or nearby are assumed to have died. Local recruitment, the recruitment of young into the adult population, occurs when offspring return to their natal site and become a part of the breeding population. Recruitment into the breeding population is often used as a proxy for fitness in studies of avian species (Saino et al., 2012).

In most species, one sex is more philopatric than the other. In the majority of birds, females typically disperse further away from their natal site than do males, making females less philopatric (Greenwood, 1980). Females may disperse further to avoid inbreeding and increase access to mates and/or resources, thereby increasing their reproductive success (Greenwood, 1980). Winkler and colleagues (2005) found that the median dispersal distance for female Tree Swallows is 2.12 times that of males. In Great Tits (*Parus major*), approximately 25% of males and 10% of females return to their natal territory to breed (Greenwood et al., 1979). In both Pied Flycatchers (*Ficedula hypoleuca*) and Great Tits, a greater proportion of males than females return to their natal site to breed (Greenwood, 1980). As adults, 93% of male Pied Flycatchers return each year to the first site they occupied as a breeder compared to 37% of adult females (Greenwood, 1980).

Predation on eggs or fledglings often prompts females to disperse to a different breeding site for subsequent breeding seasons (Greenwood, 1980). After successful breeding attempts, both males and females typically return to the same breeding site where they were successful (Winkler et al., 2004; Greenwood, 1980). However, this assumption has been challenged by Shutler and Clark (2003) who found that adult and natal dispersal distances were not significantly influenced by breeding success in Tree Swallows. Shutler and Clark (2003) manipulated reproductive success and found it had no effect on subsequent dispersal in Tree Swallows.

It has been consistently reported that clutch size decreases as the breeding season progresses in Tree Swallows (Stutchbury & Robertson, 1987), Great Tits (Perrins & McCleery, 1989), Barn Swallows, (*Hirundo rustica*) (Grüebler & Naef-Daenzer, 2008), and Purple Martins (*Progne subis*) (Tarof et al., 2011). Although the cause responsible for this decrease in Tree

Swallow clutch size has not received as much attention as that of the Great Tit. Research suggests clutch size in the Great Tit decreases seasonally because caterpillars, their main food source, become scarcer as the breeding season progresses (Perrins & McCleery, 1989).

In Tree Swallows, it has been suggested that the decline in clutch size may result from less experienced birds breeding later in the season and producing smaller clutches relative to more experienced birds (Stutchbury & Robertson, 1987; Winkler & Allen, 1996). First time breeders, such as second-year (SY) females, return to the breeding site later than more experienced birds, such as after-second-year (ASY) females (Winkler & Allen, 1996). However this has been challenged by the findings of Stutchbury and Robertson (1987), who found that both SY and ASY females laid fewer eggs as the breeding season progressed.

It has also been hypothesized that a decrease in insects, the main food source of Tree Swallows, may be responsible for the within-season decline in reproductive performance (Stutchbury & Robertson, 1987). This has been challenged by evidence that food abundance does not often affect nestlings due to the parents incurring the costs of a depleted food supply (Dunn et al., 2011). Food abundance varies greatly with geographic area, and evidence has been found that even in areas where food supply increases over the breeding season there still exists a decline in the reproductive success of Tree Swallows (DeSteven, 1978; McCarty & Winkler, 1999). Therefore implying that food abundance alone is not responsible for the decline in reproductive performance seen in Tree Swallows as the breeding season progresses.

Reproductive output is better understood when considering the number of offspring that survive to breed themselves or return as recruits, rather than simply the number of eggs or fledglings that are produced (Greenwood et al., 1979). The aim of the present study is to unravel the factors that affect the local recruitment of Tree Swallows. A greater understanding of local recruitment is important due to its implications on the lifetime reproductive success of breeding adults. We set out to investigate whether the sex of the fledgling, age of the mother, physical characteristics of the parents, family size, or time of season at hatching were associated with the likelihood that a Tree Swallow fledgling would become a recruit.

Methods

Study Species

The Tree Swallow is a secondary cavity-nesting insectivore that spends its winters in Florida, the Caribbean and along the Gulf of Mexico (Robertson et al., 1992). Each spring Tree Swallows fly north to their breeding range throughout central and northern North America (Robertson et al., 1992). Other than the annual migration of Tree Swallows between breeding site and wintering range, there is little within-season movement between territories (Robertson et al., 1992).

Tree Swallows readily take up residence in nest boxes and have been deemed a “model species” due to their resiliency to human interaction (Robertson et al., 1992). Tree Swallows are uncommonly resistant to human disturbance, making them easy to trap and measure (Winkler et al., 2004). The age of a female Tree Swallow is easily determined based on the coloration of her plumage; SY females are brown, after-hatching-year (AHY) females are 50% brown and 50% blue-green, and ASY females are iridescent blue-green in color (Robertson et al., 1992).

Tree Swallows are typically philopatric, returning to their natal site each year to reproduce. Recapture of nestlings as returning adults is frequently used as an indicator of post-fledging survival and recruitment (McCarty, 2001). It is possible that this method underestimates the survival rate of Tree Swallow fledglings but a more thorough investigation would require rigorous fieldwork carried out in all nearby areas and subpopulations. We utilized very refined success data (considering only parents who produced one or more recruits successful), which may have been restrictive to our analyses. However, our design serves the purpose of identifying recruits and understanding the factors that affect local recruitment in Tree Swallows.

Male Tree Swallows typically return to the breeding site several days prior to the females to secure a nest cavity or nest box, and assert their territory surrounding the nest site (Robertson et al., 1992). Tree Swallows are a single-brooded species that lay the majority of their eggs in May (Robertson et al., 1992). Young fledge from the nest between mid-June to mid-July, some fledging as late as August (Robertson et al., 1992).

Study Site

We studied Tree Swallows breeding in the nest boxes at Grand Valley State University (GVSU), Ottawa County, Michigan (42˚ 57' N, 85˚ 53' W). The study site consisted of open fields with several shallow bodies of water. Tree Swallows readily take up residence in nest boxes that are located around fields and near water (Robertson et al., 1992). The present study is a part of a larger, on-going study conducted by Dr. Michael Lombardo at Grand Valley State University. We report on observations gathered during the breeding seasons from 1992 to 2006. Data analyses are limited to years 1992 to 2006 due to extensive nest predation in 2006, which significantly reduced the number of birds returning the following year. The extensive nest predation prevented us from capturing and identifying many adults and banding nestlings. The nest predation also destroyed such a great number of nests largely altering the number of birds that survived to return the following year and therefore would not provide accurate information.

Field Methods

At the beginning of the breeding season each year, nest boxes were emptied and repaired if necessary. The standard wooden nest box was used. The nest boxes were 25 meters apart on average. Tree Swallows occupied most of the nest boxes throughout the season but not all were used. We extensively monitored 100 nest boxes where the Tree Swallows had nested each breeding season. The activity occurring at each nest box was carefully recorded each morning between 8:00AM EST and 2:00PM EST. Day was recorded using Julian dates, 1 = 1 January.

After clutch initiation date and clutch size were recorded, visits were timed to determine hatching and fledging success. Adult birds were captured opportunistically after their young were hatched to record their band number or band unknown birds. The nestlings were collected and measured at nestling days 3, 6, 9, 12, and 20. A suite of physical characteristics of both the nestlings and the parents were measured and recorded.

All procedures involving birds were approved by the Grand Valley State University Institutional Animal Care and Use Committee to ensure the birds were not harmed nor their behavior disrupted.

Statistical Analyses

Data was analyzed using SPSS 12.01 for Windows (SPSS, 2003). In the majority of our statistical analyses we selected only cases where the Tree Swallow was an adult female in order to count each nest accurately without duplicates. Adult females and the number of recruits each produced were used to calculate the total number of recruits produced to eliminate double counting. We eliminated after-hatching-year (AHY) females from the majority of our analyses due to the small sample size. We also eliminated nests with a brood size at hatching (BSH) of 0 for many of our analyses because our main interest was the production of recruits, which cannot come from nests without nestlings.

Chi-square tests were used for testing the null hypothesis between BSH and whether or not a recruit was produced, female age and whether or not a recruit was produced, and female age and the number of recruits produced. Independent samples t-tests were used to compare the sample means between individuals that did and did not produce a recruit for each sex and female age. A non-parametric Mann-Whitney test was ran on clutch initiation dates and whether or not a recruit was produced to determine whether the median clutch initiation date was larger for one group compared to the other. A median test was ran to compare the clutch initiation dates of nests that produced recruits with those that did not produce recruits. Frequency tables were created for nests with each BSH and brood size at fledging (BSF) to provide the number of nests that did and did not produce one or more recruits. Frequency tables were also created for clutch sizes, brood sizes at hatching , brood sizes at fledging, recruits, and recruits grouped by their mother's age. A logistic regression was conducted to determine the relationship between clutch initiation date and whether or not a recruit was produced. A analysis of variance (ANOVA) was conducted to detect a correlation between clutch initiation date and clutch size.

Results

Among 780 nests observed between 1992 and 2006, 4682 eggs were laid in total. 73.96% of those eggs hatched into the 3463 nestlings that we carefully monitored and measured over the course of our study. 131 nests produced no nestlings. 70.63% of the nestlings fledged; 2446 fledglings in total. 77.31% of nests produced at least one fledgling (N=603). Of 603 nests that produced fledglings, 4.06 nestlings fledged per nest on average. Of 2446 Tree Swallow fledglings, only 166 (14.73%) returned to the study site as a recruit. However, when considering all nestlings (N=3463) only 4.79% became recruits (N=166). Although the number of recruits is exact (N=166), the number of nestlings that fledged may be slightly inaccurate due to failure to record BSF for each nest. We found a total of 166 recruits, although Table 1 only shows 164 because the mothers of 2 recruits were not captured and recorded.

Distribution of Recruits

As shown in Table 1, 780 nests were observed over the years 1992 to 2006, with the majority of nests (N=644) producing no recruits. Less than one recruit (0.21) was produced per nest. Only 17.43% of nests produced one or more recruits, while the remaining 82.56% of nests produced no recruits (Table 3). 115 nests produced 1 recruit, 15 nests produced 2 recruits, 5 nests produced 3 recruits, and 1 nest produced 4 recruits (Table 1). 70.12% of recruits were the only fledgling that survived from their nest (N=115). 18.29% of recruits were 1 of 2 that survived from one nest (N=30). The distribution of recruits is not significantly different than expected by chance and the frequency of each brood size.

Sex Ratio of Recruits

Of 166 recruits, 79 were male, 70 were female, and 17 were unknown (Table 2). Table 2 shows that 47.59% of recruits were male and 42.17% of recruits were female, although this difference is not significantly different from 50:50. However, we are assuming that the sex ratio at fledging is the same at recruitment, which may not be the case. 10.24% of recruits were unable to be sexed (n=17). The birds for which sex is unknown were found dead and were iridescent blue-green in color, making them indistinguishable between a male and an ASY female.

Family Size

Brood size at hatching (BSH) provides insight into the environmental conditions within the nest as the nestlings developed, as it is in essence the size of the family. In the present study, the average BSH was 4.44±1.32 (N=780). Most nests had a BSH of 4, 5 or 6; N=191, 261, and 154 respectively. The 166 recruits came from 136 nests (Table 3 shows 164 recruits due to failure to capture 2 mothers). Both the greatest number of nestlings (N=1305) and recruits (N=70) were produced by broods of 5, the most common brood size (33.46% of nests) found in our sample of Tree Swallows (Table 3). Although the greatest number of recruits came from broods of 5, broods of 7 were the most likely to produce recruits (30%) (Table 3). The greatest percent of nestlings that became recruits (7.69%) was found in broods of 1, although closely followed by broods of 7 (7.14%) (Table 3). The largest brood size recorded was of 8, found in only 2 nests and resulting in no recruits (Table 3).

Two nests of a BSH of 1 produced a recruit, 4 nests of a BSH of 2 produced 1 or more recruits, 9 nests of a BSH of 3 produced 1 recruit, 34 nests of a BSH of 4 produced 1 or more recruits, 55 nests of a BSH of 5 produced between 1 and 4 recruits, 29 nests of a BSH of 6 produced between 1 and 3 recruits, 3 nests of a BSH of 7 produced 1 or more recruits, and no nests of a BSH of 8 produced recruits (Table 3). Two nests of a BSF of 1 produced 1 recruit, 5 nests of a BSF of 2 produced 1 or 2 recruits, 8 nests of a BSF of 3 produced 1 recruit, 34 nests of a BSF of 4 produced 1 or 2 recruits, 44 nests of a BSF of 5 produced between 1 and 4 recruits, 24 nests of a BSF of 6 produced between 1 and 3 recruits, and 1 nest with a BSF of 7 produced 1 recruit.

Our sample provided us 780 data points for BSH. We found no significant difference between BSH and whether or not a recruit was produced (all p>0.05). We then organized the data into categories based on BSH to increase the number of cases in each cell. The categories were BSH of 1-3, 4, 5, 6, and 7-8. We then found a significant difference between BSH and whether or not a recruit was produced (x^2(4)=10.63, p<0.05). But when we only included the 479 cases of nests with a BSH of 4, 5, or 6 (the most common in our study) the relationship between BSH and the likelihood a recruit was produced or not was no longer significant (G(2)=1.26, p=0.53). Therefore the likelihood of producing is not influenced by family size across the most common family sizes (BSH) of 4, 5 or 6.

Mother's Age

We conducted a chi-square test on female age and the number of recruits produced and found no significant effect, G(4)=3.78, p=0.44. When we compared the likelihood SY and ASY females would produce a recruit we found no significant difference, x^2=(1, N=773)=3.47, p=0.06. We did not compare AHY females due to the small size of the sample. Of 199 SY females, 12.56% (N=25) produced one or more recruits. Of 574 ASY females, 18.29% (N=105) produced one or more recruits. Although we found that ASY females produced more recruits than SY females, this difference in reproductive success was not statistically significant (p>0.05). 174 SY females produced no recruits, 20 produced 1 recruit, and 5 produced 2, 3 or 4 recruits. While 469 ASY females produced no recruits, 89 produced 1 recruit, and 16 produced 2, 3 or 4 recruits. Although not significant, more ASY females produced more than 1 recruit compared to SY females, x^2(2, N=773)=3.74, p=0.15. Overall, our results show that the age of a fledgling's mother does not significantly affect its likelihood of becoming a recruit.

Parental Physical Characteristics

We compared SY females, AHY females, ASY females, and males who did and did not produce one or more recruits on various physical characteristics. The traits considered included right tarsus length, bill length, right wing length, right tail length, mass, and the total louse holes found in wing and tail feathers.

Table 4 shows that for both SY females and ASY females, total louse holes was significant originally, but once equal variances were not assumed the p-value was no longer significant (p=0.63, p=0.11 respectively). Therefore, for SY and ASY females, the total number of louse holes found in their feathers only approached a significant difference between females that produce at least one recruit compared to those that do not produce any.

The sample of AHY females was notably smaller than the other female samples, with between N=35 to 38, depending on the measure (Table 4). The number of total louse holes found in their feathers was found to differ significantly between AHY females that produced one or more recruits versus those that did not, however the sample was very small. For males, both right tail length and total louse holes approached significance. Aside from the finding in AHY females, there exist no significant differences between the parents that produce recruits compared to those that do not produce recruits.

Time of Season

Of the 633 nests that produced no recruits, the average date of clutch initiation was day 139.04. For the 134 nests that produced one or more recruits, the average date of clutch initiation was day 137.05, more than one day earlier than nests that produced no recruits. However, it must be noted that clutch initiation date was not collected for all recruits.

In our sample, the median clutch initiation date was day 137. A median test was conducted using BSH and showed that of the nests that produced recruits, 78 nests had clutch initiation dates prior to the median (day 137), while 57 nests had clutch initiation dates after the median. Although not statistically significant, this shows that more recruits were hatched earlier than the median clutch initiation date than after.

When considering all nests, including those unsuccessful at producing nestlings or fledglings, the mean clutch initiation date is day 138.77±10.01, with the earliest clutch initiation date day 122 and the latest day 180. When we conducted another median test, to include only nests that produced at least one nestling, the median clutch initiation date remained the same (day 137) but the mean was slightly earlier, day 138.69±10.00. We found no significant difference in the clutch initiation dates between those nests that produced recruits and those that did not (M-W U=39447.5, p=0.20). When we conducted the median test for a third time, only considering nests that produced at least one fledgling, the median was one day earlier, day 136. For nests that produced at least one fledgling, the mean clutch initiation date was 138.88±10.24.

Using logistic regression we found a significant relationship between clutch initiation date and whether or not the nest produced a recruit for all nests (including a BSH of 0), $x^2(1, N=901)=4.72$, $p=0.03$. When we refined the regression and only included nests that had a BSH of at least 1 and found a significant relationship between clutch initiation date and whether or not a recruit was produced, $x^2(1, N=767)=4.65$, $p=0.03$. Finally we did the regression again, only including nests with a BSF of at least 1 (because only those juveniles that fledged have a chance of becoming recruits) and again found a significant relationship, $x^2(1, N=594)=6.36$, $p=0.01$. Therefore, the relationship between clutch initiation date and the likelihood of producing recruits is significant for all nests.

There was a significant effect of clutch initiation date on clutch size using a one-way ANOVA (F_1=114.95, p=0.00). We found clutch size was negatively correlated with clutch initiation date (r=-0.34, p=0.00), and this finding was statistically significant.

Discussion

We found a local recruitment rate of 4.79% between the years of 1992 and 2006, when considering all Tree Swallow nestlings (N=3463). 14.73% of fledglings (N=2446) became a recruit. Over the course of our study we identified 166 recruits. Shutler and colleagues (2006) also studied local recruitment in Tree Swallows and reported 4.7% of nestlings returned as recruits, regardless of the experimental manipulation endured at hatching. Between 1985 and 1998, Winkler and colleagues (2005) reported a local recruitment rate of 2.98% in their sample of Tree Swallows.

Distribution of Recruits

The majority of nests do not produce recruits (N=644; Table 1). The production of recruits is important because it increases the lifetime reproductive success of the parents responsible. 70.12% of the recruits produced were the only surviving fledgling from one nest (Table 1). This is reasonable considering that recruits must survive migration to their wintering range, predation and competition as well as make it back to their natal site to reproduce. Although rarely, more than one recruit is produced within the same nest, which was true for 21 nests in our sample (Table 1).

In our study, 30 recruits (18.29%) were 1 of 2 surviving fledglings from one nest (Table 1). Shutler and Clark (2003) reported that 58 of 203 recruits (28.57%) were pairs of siblings in Tree Swallows. They suggested this high proportion of sibling recruits pointed to a genetic predisposition for low dispersal or high survival due to high quality parents (Shutler & Clark, 2003). We also found 15 recruits (9.14%) were 1 of 3 surviving fledglings from one nest and 4 recruits (2.44%) were produced by one nest (Table 1).

Greenwood and colleagues (1979) found that in Great Tits, most breeding attempts result in either no offspring or one individual that survives to recruit. In Great Tits, it has been recorded that up to 5 recruits were produced by a single nest compared to the present study where we found the maximum number of recruits produced by a single Tree Swallow nest was 4 (Greenwood et al., 1979).

Sex Ratio of Recruits

In the present study, we found the sex ratio of Tree Swallow recruits was not significantly different from 50:50 (Table 2). However, we did not consider any Tree Swallows nesting in nearby areas. This may have underestimated the survival rate reported for our nestlings because female Tree Swallows are known to disperse more often than males, although this would not affect the number of recruits, which is our main focus (Winkler et al., 2005; Greenwood, 1980).

Of 630 Tree Swallow recruits considered by Winkler and colleagues (2005), 355 were female, 257 were male and 18 were unknown. Winkler and colleagues (2005) found more female recruits than males, although the authors state this may be a result of females being easier to capture. Whittingham and Dunn (2000) reported that the sex ratio within each brood of Tree Swallows is significantly male biased (57% male). However, the sex ratio within each brood may not be the same for those that fledge or become recruits.

In Tree Swallows, a male-biased sex ratio is related to the mother being in better body condition with lower parasite loads (Whittingham & Dunn, 2000). It has been hypothesized that male offspring may increase a mother's lifetime fitness more than a female because male nestlings grow faster and reach a higher mass compared to females, which increases their likelihood of survival and subsequent recruitment (Whittingham et al., 2007).

Because female Tree Swallows are more likely to disperse to a new breeding site as compared to males, there is a possibility that the number of females that survived is underestimated because we only considered those who returned to our study site. Males may be more likely to return to their natal site and become a recruit than females because it is beneficial for a male to return to a habitat of which he possesses knowledge of local conditions, also being more likely to secure a territory (Delestrade et al., 1996).

Due to intraspecific competition, population density becomes a major determinant of local recruitment versus dispersal in the Great Tit (Delestrade et al., 1996). In many avian species, females tend to disperse further than males; this may be due to higher competition amongst male conspecifics than females (Delestrade et al., 1996; Greenwood, 1980). Overall, the greater likelihood of female Tree Swallows to disperse further from their natal site would result in more males returning as recruits (assuming equal survival rates). However, we did not find evidence of this in the present study, as the recruit sex ratio was not significantly different from 50:50.

Family Size

Clutch size in Tree Swallows ranges from 2 to 8 eggs, with clutches of 4 to 7 being the most common (Robertson et al., 1992). Both the greatest number of nestlings (N=1305) and recruits (N=70) were produced by broods of 5, the most common brood size (33.46% of nests) found in our sample (Table 3). Stutchbury and Robertson (1978) found that for Tree Swallow clutches of 4 or 5 eggs there was no significant decrease in the number of nestlings that fledged as the season progressed, which would suggest that the ability to care for particular brood size does not vary seasonally.

Although the greatest number of recruits came from broods of 5, broods of 7 were the most likely to produce recruits, with 30% of nests with a BSH of 7 producing one or more recruits (Table 3). This is somewhat surprising since broods of 7 are near the maximum brood size produced by Tree Swallows naturally. The greatest percent of nestlings that became recruits (7.69%) was found in broods of 1 (Table 3). Shutler and colleagues (2006) found that clutches of 3 or fewer were commonly abandoned by Tree Swallows, perhaps due to females being less motivated to incubate clutches of low reproductive value. We found no evidence of this in the present study.

Lifetime reproductive success was higher for individuals that produced clutches larger than those produced naturally (i.e. those inflated due to manipulation) (Shutler et al., 2006). Tree Swallow breeding pairs fledged more offspring from larger broods, up to a brood size of 10 (Shutler et al., 2006). Both parents increased feeding rates for larger clutches but per capita feeding rate decreased as brood size increased (Shutler et al., 2006). Because larger broods suffered lower per capita feeding rates this resulted in smaller nestlings, which may have lead to delayed fledging from larger broods. However, in the current study we found that brood sizes of 7 had the greatest likelihood of producing one or more recruits.

Shutler and colleagues (2006) manipulated clutch size in Tree Swallows prior to incubation and found that the parents were capable of hatching and fledging clutches larger than those originally laid, although the maximum was found to be 10. However a large part of the potential benefits from producing larger clutches is lost to costs in time; longer total laying time, longer hatching time, and slower nestling growth all delay the date of fledging and late-fledged young are less likely to recruit locally (Shutler et al., 2006). Tree Swallows do not produce larger clutches because they are constrained in finding sufficient food to initiate breeding early and constraints in time require that they end laying earlier so that their offspring may recruit successfully (Shutler et al., 2006).

Shutler and colleagues (2006) did not find evidence of any fitness consequences associated with raising larger broods in Tree Swallows, even when experimentally enlarged by adding 3 eggs. Therefore, they predicted directional selection for larger clutch sizes in Tree Swallows (Shutler et al., 2006). However, Wiggins (1990) found that experimentally enlarged broods of Tree Swallows suffered significantly lower masses at nestling day 16. In Tree Swallows, larger clutches are fed less per capita resulting in smaller nestlings with lower chances of recruitment (Shutler et al., 2006). Offspring quality is affected by brood size and therefore may constrain the number of eggs Tree Swallows produce (Wiggins, 1990).

Female Great Tits that naturally produce larger broods tend to be more successful in producing recruits compared to females that produce smaller broods (Pettifor et al., 2001). In Great Tit nests where a nestling was experimentally removed, the remaining nestlings had a significantly higher mean mass at fledging than control nests (Pettifor et al., 2001). In Great Tits, increases in brood size reduce the likelihood of a nestling's survival (Perrins & McCleery, 1989). Recruitment in Great Tits was greatest for nests that raised their natural number of nestlings (Pettifor et al., 2001). Great Tit broods where a nestling was experimentally added did not experience a significant difference in offspring recruitment compared to control broods (Pettifor et al., 2001). In Purple Martins, large broods experience relatively low fledgling survival (Tarof et al., 2011). Grüebler and Naef-Daenzer (2008) found Barn Swallow breeding pairs only fledge one brood because the costs associated with a late second brood exceed the benefits.

Winkler and Allen (1996) and Dawson (2008) found evidence suggesting female Tree Swallows adjust their clutch size seasonally as a strategic adjustment to the declining prospects of offspring survival as the season progresses, rather than their clutch size being dictated by their physical condition. The offspring hatched later in the season are determined to be less valuable because they are less likely to become recruits (Winkler & Allen, 1996). Because offspring hatched later in the season are of lower quality, females often decide to avoid having larger clutches because the last eggs will be hatched later in the season (Shutler et al., 2006; Winkler & Allen, 1996) In Tree Swallows, adult females forgo having more, less-valuable offspring and conserve their energy and resources for self-maintenance and subsequently increasing the likelihood they will survive to reproduce the following breeding season (Dawson, 2008; Winkler & Allen, 1996).

Mother's Age

Although we found that ASY females produced more recruits than SY females, this difference was not statistically significant ($p>0.05$). More ASY females ($N=16$) produced more than 1 recruit compared to SY females ($N=5$), but again this difference was not statistically significant ($p>0.05$). Although differences between older, more experienced females and younger females exist, the effects of a mother's age on the likelihood of producing a recruit were not statistically significant in our sample of Tree Swallows.

Greenwood and colleagues (1979) reported that in Great Tits, older females had a higher reproductive success compared to first-time breeders. The reproductive success of female Great

Tits in their first breeding year was affected by year, laying date and clutch size (Visser & Verboven, 1999). In Purple Martins, ASY females typically arrived at the breeding site and initiated nesting about 2 weeks prior to SY females (Tarof et al., 2011). Therefore, in Purple Martins young fledged earlier in the season typically had older mothers (Tarof et al., 2011).

Stutchbury and Robertson (1987) studied Tree Swallows and found that early in the breeding season, ASY females had an average clutch size one-half egg greater than that of SY females. Early in the season, ASY females also had greater hatching and fledgling success compared to SY females, but this difference diminished as the season progressed (Stutchbury & Robertson, 1987). It has been hypothesized that the increased foraging efficiency of SY females as the season progresses may explain these findings, and therefore eliminate the initial difference between the two age groups.

After-second-year females were found to be more successful in raising broods of 5 or 6 compared to SY females (Stutchbury & Robertson, 1987). Winkler and Allen (1996) found evidence that female age and wing length were the only significant predictors of laying date in Tree Swallows. Female age and laying date predicted clutch size in Tree Swallows (Winkler & Allen, 1996). Breeding females that were younger and/or had shorter wings tended to breed later and females that laid later had smaller clutches regardless of their physiological condition (Winkler & Allen, 1996).

Ardia and Clotfelter (2007) found that higher quality female Tree Swallows initiated laying earlier in the season and their nestlings were in better condition. The lower quality females that laid their eggs later in the season were less able to deal with the energetic costs associated with having their feathers clipped experimentally; they reduced the time spent incubating their clutch relative to females who laid earlier and also had their feathers clipped (Ardia & Clotfelter, 2007).

It is suggested that older Tree Swallow females are better at: gathering the necessary resources for reproduction, obtaining mates and nest cavities early on in the breeding season, building nests, incubating eggs, and feeding nestlings (Winkler & Allen, 1996). This relationship may be mediated by breeding experience rather than age itself (Winkler & Allen, 1996).

Stutchbury and Robertson (1987) concluded that the within-season decline in reproductive performance in Tree Swallows is not simply due to younger birds breeding later, since this decline was seen in all ages of female breeders. The decline in reproductive performance as the breeding season progressed was related to the time of the season, rather than parental care characteristics or the age of the mother (Stutchbury & Robertson, 1987).

Parental Physical Characteristics

We found no evidence that differences in the physical characteristics of Tree Swallow parents were responsible for whether or not a recruit was produced. Winkler and Allen (1996) concluded that the physiological condition of the female played a minor role in clutch size and its seasonal decline found in Tree Swallows. Ardia and Clotfelter (2007) found that upon experimentally clipping the wings of female Tree Swallows, the females lost body mass, suggesting that feather clipping reduced foraging efficiency. However, we found no evidence that females with shorter wings had a reduced ability to raise nestlings or produce recruits. Disruptive selection on female tarsus length has been reported in Tree Swallows in past literature, however we found no evidence of this in the present study (Wiggins, 1991).

Although in Great Tits, Perrins and McCleery (2001) found that lighter females laid slightly earlier in the season than heavier females; we found no evidence of this in Tree Swallows. Sanio and colleagues (2012) suggested that the phenotypic quality of Barn Swallow parents might decline as the breeding season progresses. However, Grüebler and Naef-Daenzer (2008) found that physiological factors could not account for between-year variation in seasonal trends in Barn Swallows.

Time of Season

The Likelihood of Producing Recruits

Of the 633 nests that produced no recruits, the average date of clutch initiation was day 139.04. For the 134 nests that produced one or more recruits, the average date of clutch initiation was day 137.05, more than one day earlier than nests that produced no recruits. Although the difference between these two groups is not statistically significant it does show that even a day or two earlier in the season may have a significant impact on reproductive success. This trend is in accordance with predictions; nests that begin laying earlier are more likely to produce recruits. Previous work on Tree Swallows has found no evidence that later-hatched chicks disperse differently than their earlier cohort members, making it unlikely that later-hatched chicks recruited elsewhere (Winkler et al., 2005).

The median clutch initiation date for nests that produced at least 1 nestling was day 137, while the median clutch initiation date for nests that produced at least 1 fledgling was day 136. Although not significant, this suggests that nests that produce fledglings may be hatched earlier in the season. Dawson (2008) found that Tree Swallows that bred earlier in the season were more successful at producing fledglings. And only nests that produce fledglings have a chance a producing one or more recruits.

We found a significant relationship between clutch initiation date and whether or not a recruit was produced for all nests (p=0.03), nests that produced at least one nestling (p=0.03), and nests that produced at least one fledgling (p=0.01). Therefore, the relationship between clutch initiation date and the likelihood of producing recruits is significant for all nests. Of the nests that produced recruits, 78 nests had clutch initiation dates prior to the median (day 137), while 57 nests had clutch initiation dates after the median. Showing that more recruits were hatched earlier than the median clutch initiation date than after. In Tree Swallows, the time of season at which the birds fledged significantly affected their likelihood of recruitment; late-fledged young were less likely to recruit locally (Shutler et al., 2006). Winkler & Allen (1996) found that offspring fledged later in the season had a lower probability of surviving to the next breeding season and subsequently a reduced chance of becoming a recruit.

Fledging and post-fledging success of offspring also declines as the season progresses (Winkler & Allen, 1996). Verboven and Visser (1998) found that in Great Tits, young fledged early in the breeding season were more likely to recruit into the breeding population than young fledged later in the season. Verboven and Visser (1998) showed that local recruitment is causally related to fledging date. After controlling for fledgling mass and brood type there was a negative effect of fledging date on recruitment in the Great Tit (Verboven & Visser, 1998).

In Purple Martins, the likelihood of survival declines sharply as fledging date and brood size increases (Tarof et al., 2011). In Barn Swallows *(Hirundo rustica)*, fledgling survival also declines as fledging date increases (Grüebler & Naef-Daenzer, 2008). A cross-fostering experiment in Barn Swallows showed that differences in post-fledging survival could not be attributed to differences in parental competence, rather regardless of treatment, post-fledging survival declined as the season progressed (Grüebler & Naef-Daenzer, 2008). This shows that environmental conditions (i.e. time of season) were the main determinant of juvenile survival in Barn Swallows (Grüebler & Naef-Daenzer, 2008). However, it remains unclear whether this seasonal decline in juvenile survival is due to food shortage, increase in predation pressure, or an alternate explanation.

Saino and colleagues (2012) found evidence of directional selection for early breeding in Barn Swallows, similar to what our findings would suggest. Barn Swallow nestlings hatched earlier in the season experienced greater longevity and higher lifetime reproductive success (Sanio et al., 2012). Visser and Verboven (1999) found that for male Great Tit recruits there was a significant effect of fledging date on their lifetime reproductive success. Male Great Tits that fledged relatively late in the season produced fewer recruits in their first year of breeding, often due to the failure to produce any fledglings (Visser & Verboven, 1999). In the Great Tit, evidence has shown that the likelihood a nestling survives decreases 3.6% per day later in the season they are hatched (Perrins & McCleery, 1989).

Visser and Verboven (1999) stated that considering the number of offspring recruited alone underestimates the fitness costs of breeding late. Early environmental conditions and maternal decisions on the time of breeding have long-term consequences on longevity and lifetime reproductive success in Barn Swallows (Saino et al., 2012).

Clutch Size

We found significant effect of clutch initiation date on clutch size in Tree Swallows (p=0.00). We found clutch size was significantly negatively correlated with clutch initiation date (p=0.00). There exists selection for earlier laying because birds that lay their eggs earlier usually have larger clutches and fledge more young (Dunn et al., 2011). Perrins and McCleery (1989) found similar evidence in Great Tits, early pairs raised more young than later ones and these nestlings are heavier and more likely to survive. In Great Tits, the likelihood of survival decreases for nestlings hatched later in the season and this trend intensifies as brood size increases (Perrins & McCleery, 1989). In Purple Martins, it has also been reported that clutch size declines as the breeding season progresses (Tarof et al., 2011).

Stutchbury and Robertson (1987) found that for both SY and ASY female Tree Swallows clutch size decreased later in the season, as well as the number of nestlings and fledglings. Winkler & Allen (1996) suggested that female Tree Swallows adjust their clutch size as a strategic adjustment to the diminishing prospects of reproductive success for eggs laid later in the season rather than adjusting clutch size based on their physical condition.

Although larger broods were more likely to produce recruits, this did not differ significantly from the expected distribution by chance. This also may be a result of higher quality parents breeding earlier in the season when clutch size is largest. Lombardo and Thorpe (2010) found evidence that clutch size and the number of fledglings produced decreased significantly with increasing clutch initiation date. Therefore it is reasonable to assume that more recruits come from larger clutches that are hatched earlier in the season.

Due to the location of our study, found in a temperate zone, there exists directional selection favoring early breeding resulting in improved reproductive success (Dunn et al., 2011;

Wiggins, 1991). Tree Swallows that bred later were less successful in raising nestlings than earlier breeding birds (Dawson, 2008). During their 2010 study, Lombardo & Thorpe found that no juvenile Tree Swallows fledged from nests where egg laying began later than 29 June. However, this directional selection is constrained by the ability of breeding birds to acquire the necessary components for their nest as well as consume the necessary nutrients to promote egg laying. Birds may not be able to lay their eggs at the ideal time due to constraints on the nutrients required for egg-laying (Perrins, 1996; Wardrop & Ydenberg, 2003). Perrins (1996) studied the Great Tit and proposed that the calcium requirement may take valuable time away from other feeding activities, instead foraging for calcium-rich, energy-poor food required for making eggshells.

Conclusion

The average lifespan of a Tree Swallow is 2.7 years (Robertson et al., 1992). Therefore each breeding attempt is very important in determining their lifetime reproductive success due to their short life span. Only offspring that become recruits and breed themselves increase the reproductive success of their parents. Of all the factors considered in the present study, only the time of season had any significant affect on the likelihood a nestling would become a recruit. The relationship between clutch initiation date and the likelihood of producing one or more recruits was significant for all nests in our sample. As the season progressed, both clutch size and the likelihood of producing at least one recruit decreased.

One possible explanation would be the “relative age effect.” The term was originally coined by Helsen and colleagues (2005) in relation to young soccer players, used to explain the physical advantages of being relatively older than others in the same age group. One age group contains individuals born throughout an entire year, therefore those born in January are more developed and more experienced than those born later in the year (Helsen et al., 2005). Just as one cohort group of Tree Swallows contains juveniles that hatched and fledged throughout the entire breeding season. This phenomena is relevant to our findings because asymmetries in the amount of time a fledgling has to mature prior to migrating south for winter may be responsible for earlier hatched nestlings having a higher likelihood of recruitment.

Late-fledged juveniles that survive to migration may incur higher subsequent mortality due to less foraging time and experience prior to migration relative to other cohort members. Juvenile mortality is more likely to affect those of lower mass and limited flight experience resulting from less foraging time as well as those less experienced with predation risk.

The “relative age effect” seems evident in Tree Swallows. Late-fledging may considerably disadvantage juveniles in surviving migration since they depart around the same time as early-fledged young, they will be considerably younger and disadvantaged at the time of migration. This asymmetry could mean that juveniles that fledged earlier have had the opportunity to acquire more experience at foraging and predator avoidance that gives them an advantage at their first migration. Dawson (2008) came to a similar conclusion, fledgling late is detrimental because a sufficient amount of time to develop and improve their body condition before migration is vital to their subsequent survival.

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Appendix

Table 1. The frequency of producing recruits in Tree Swallows and the distribution of recruit production among 780 nests from 1992 to 2006 at our study site at GVSU.

Number of Recruits	*Number of Nests*	*Number of Recruits Produced*	*Percent of Recruits Produced (%)*
0	644	0	0
1	115	115	70.12
2	15	30	18.29
3	5	15	9.14
4	1	4	2.44
Total	*780*	*164*	

Table 2. The sex ratio of the Tree Swallow recruits recorded from 1992 to 2006 at GVSU.

Sex	Number of Recruits	Percent of Recruits (%)
Males	79	47.59
Females	70	42.17
Unknown	17	10.24
Total	166	

Table 3. The number and percent of nests with each brood size at hatching that did and did not produce recruits and the number of nestlings and recruits produced between 1992 and 2006 at the GVSU.

Brood Size at Hatching (BSH)	*# of Nests*	*# of Nests that Produce 0 Recruits*	*# of Nests that Produce 1+ Recruits*	*# of Nestlings*	*# of Recruits*	*% of Nests*	*% of Nests that Produce 0 Recruits*	*% of Nests that Produce 1+ Recruits*	*% of Nestlings That Become Recruits*
1	26	24	2	26	2	3.33	92.31	7.69	7.69
2	50	46	4	100	5	6.41	92	8	5
3	86	77	9	258	9	11.03	89.53	10.47	3.49
4	191	157	34	764	36	24.49	82.2	17.8	4.71
5	261	206	55	1305	70	33.46	78.93	21.07	5.36
6	154	125	29	924	37	19.74	81.17	18.83	4
7	10	7	3	70	5	1.28	70	30	7.14
8	2	2	0	16	0	0.26	100	0	0
Total	*780*	*644*	*136*	*3463*	*164*				

Table 4. Physical characteristics of Tree Swallow parents that produced 1 or more recruits compared to those that did not produce a recruit; Mean±1 Standard Deviation, Sample Size (N).

	Physical Characteristic	***Produced No Recruits***	***Produced 1 or More Recruits***	***F, p-value*** [a]
Second-Year (SY) Female	Right Tarsus Length	12.10±0.43, N=114	11.97±0.45, N=21	0.01, p=0.93
	Bill Length	6.56±0.44, N=115	6.50±0.42, N=21	0.15, p=0.70
	Right Wing Length	109.61±2.45, N=114	109.95±2.33, N=21	0.72, p=0.40
	Right Tail Length	9.09±2.23, N=111	8.95±2.16, N=21	0.01, p=0.95
	Mass	19.54±1.90, N=116	19.66±1.75, N=21	0.02, p=0.88
	Total Louse Holes	5.68±7.58, N=108	7.00±11.51, N=19	5.62, p=0.02; t=-0.48, p=0.63
After-Hatching-Year (AHY) Female	Right Tarsus Length	12.27±0.55, N=36	11.86±0.35, N=5	1.02, p=0.32
	Bill Length	6.50±0.57, N=37	6.32±0.37, N=5	0.97, p=0.33
	Right Wing Length	110.38±2.58, N=37	109.40±2.30, N=5	0.09, p=0.76
	Right Tail Length	8.39±1.79, N=36	9.40±1.67, N=5	0.08, p=0.78
	Mass	19.51±2.03, N=38	19.04±1.10, N=5	1.22, p=0.28
	Total Louse Holes	5.11±8.73, N=35	14.40±11.95, N=5	0.37, p=0.55; t=-2.13, p=0.04*
After-Second-Year (ASY) Female	Right Tarsus Length	12.13±0.50, N=361	12.13±0.47, N=69	0.09, p=0.76
	Bill Length	6.49±0.47, N=367	6.50±0.46, N=71	0.24, p=0.62
	Right Wing Length	111.63±3.02, N=370	112.06±2.64, N=70	1.72, p=0.19
	Right Tail Length	9.72±5.81, N=354	9.58±2.01, N=67	0.07, p=0.79
	Mass	20.09±2.02, N=395	20.15±2.06, N=80	0.66, p=0.42
	Total Louse Holes	3.26±6.78, N=356	5.17±9.02, N=65	8.64, p=0.01; t=-1.62, p=0.11
Male	Right Tarsus Length	12.16±0.49, N=473	12.14±0.64, N=93	0.57, p=0.45
	Bill Length	6.53±0.43, N=499	6.50±0.46, N=106	0.01, p=0.94
	Right Wing Length	115.75±3.21, N=498	116.12±3.21, N=106	0.03, p=0.86
	Right Tail Length	10.89±2.29, N=471	10.77±1.99, N=104	4.50, p=0.03; t=0.55, p=0.58
	Mass	20.13±1.24, N=514	20.04±1.31, N=108	0.42, p=0.52
	Total Louse Holes	4.70±8.50, N=485	5.84±10.81, N=105	5.54, p=0.02; t=-1.01, p=0.31

[a]=For cases that were significant according to Levene's Test of Equal Variances. Equal variance was not assumed and the t-values, degrees of freedom, and p-value are listed for the Independent Samples T-Test.
*=Statistically significant; p-value ≤ 0.05