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Authors: Monroe, Adrian P., Hallinger, Kelly K., Brasso, Rebecka L., and Cristol, Daniel A.

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OCCURRENCE AND IMPLICATIONS OF DOUBLE BROODING IN A SOUTHERN POPULATION OF TREE SWALLOWS

ADRIAN P. MONROE, KELLY K. HALLINGER, REBECKA L. BRASSO, AND DANIEL A. CRISTOL[1]

Institute for Integrative Bird Behavior Studies, Department of Biology, College of William & Mary, Williamsburg, VA 23187

Abstract. Double brooding is the initiation of a second clutch of eggs after successfully raising young from the first clutch. Migratory birds that nest in temperate North America are often single-brooded, but there is widespread intra- and interspecific variation. Tree Swallows (*Tachycineta bicolor*), which are becoming a model species in biology, are typically classified as a single-brooded species. We documented 18 cases of double brooding in a population of Tree Swallows recently established in the Shenandoah Valley, Virginia. Double brooding may be underreported in this species or may be increasing as a result of climate change or range expansion. If double brooding is as common elsewhere as it was in our study population, it could significantly alter estimates of seasonal or lifetime reproductive success in this widely studied bird.

Key words: ***double clutching, double brooded, productivity,*** Tachycineta bicolor*, Tree Swallow.*

Ocurrencia e Implicaciones de la Anidación Doble en una Población del Sur de *Tachycineta bicolor*

Resumen. La anidación doble es el inicio de nidadas adicionales después de un intento reproductivo exitoso. En general, las aves migratorias que se reproducen en la zona templada de América del Norte intentan sólo una nidada por temporada, pero hay mucha variación intraespecífica e interespecífica. La golondrina *Tachycineta bicolor*, que ya empieza a convertirse en una especie modelo en biología, es típicamente clasificada como una especie que intenta una sola nidada por temporada. Hemos documentado 18 casos de nidadas dobles en una población de esta especie que se estableció hace poco en el valle de Shenandoah, Virginia, Estados Unidos. Las nidadas dobles podrían haber sido insuficientemente documentadas en esta especie, o podrían estar haciéndose más frecentes como consecuencia del cambio climático o de la expansión en su rango de distribución. Si las nidadas dobles son tan comunes en otras partes como en la población que estudiamos, las estimaciones del éxito reproductivo estacional o toda la vida en esta especie ampliamente estudiada podrían cambiar significativamente.

Manuscript received 14 February 2007; accepted 9 April 2008.
[1]E-mail: dacris@wm.edu

Double brooding is the laying of a second clutch after successfully fledging nestlings from a first clutch. It is characteristic of many bird species and has been reported even in birds long classified as single-brooded (e.g., the Wrentit [*Chamaea fasciata*], Geupel and DeSante 1990; and the Orchard Oriole [*Icterus spurious*], Ligi and Omland 2007). There is little consensus as to which environmental factors favor the evolution or maintenance of this important life-history trait, but some proposed explanations include variation in food availability (Gavin 1984, Moore and Morris 2005, Nagy and Holmes 2005), parental investment strategies (Blancher and Robertson 1982, Verboven et al. 2001), or length of breeding season (Hussell 1983). Double brooding is a life-history decision that has the potential to dramatically increase reproductive output, and thus it is important to know whether this strategy is available to members of a population. If some individuals are double brooded while others are not, uncovering the factors responsible for this behavioral alternative will provide a better understanding of a species' life history.

Tree Swallows (*Tachycineta bicolor)* are insectivorous migratory birds that breed in the northern half of North America. Because Tree Swallows readily adopt artificial nest cavities, they are becoming a model species in biology, particularly in studies of life history and environmental contaminants (Jones 2003, Ardia 2005, Shutler et al. 2006). Tree Swallows are generally classified as single brooded (Robertson et al. 1992); however, rare instances have been documented in which a female laid and raised two clutches of eggs in the same season (Massachusetts, Chapman 1955; Ontario, Canada, Hussell 1983, 2003a).

It has been suggested anecdotally that some Tree Swallows in the southern portion of their range may be double brooded (Clapp 1997). This could be a new phenomenon resulting from climate change or southward range expansion. Alternatively, double brooding may have been overlooked in this species if researchers have not been in the habit of rechecking successful nest boxes. After observing two second clutches in a newly established population of Tree Swallows in Virginia, we monitored all late nests in the following two breeding seasons. Our objectives were to determine whether the females in our population were double brooding with more regularity than has previously been reported and whether double-brooded females increased their single season reproductive success.

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METHODS

This study took place during the 2006 and 2007 breeding seasons, after a pilot study during the establishment of a nest box trail in 2005. We monitored all nest boxes for the duration of each breeding season to determine whether adults with successful first broods were raising second broods. Because the 2005 field season was an unplanned pilot study in the first year of a new nest box trail, data are included only where noted.

STUDY AREA AND NEST BOXES

We erected nest boxes at 36 sites along the South, North, and Middle Rivers in Augusta and Rockingham counties, Virginia, as part of a larger study of mercury contamination (centroid: 38°10′N, –78°59′W). We assumed that, prior to our study, few Tree Swallows nested in the study area. This is based on the lack of suitable wetland habitat and our observation of only three Tree Swallow nests outside of our nest box trail during the study. In 2005, we provided 233 nest boxes. The total number of nest boxes increased to 286 before the 2006 breeding season, and to 347 for 2007. Nest boxes were placed in cropland or pasture, within 200 m of each river and approximately 25 m apart. We used a popular bluebird nest box design (North American Bluebird Society 2007) and fitted each with a "stovepipe" predator guard (Erva Tool, Chicago, Illinois), which almost entirely eliminated predation (e.g., nest failure due to predation, abandonment, and House Sparrow [*Passer domesticus*] disruption was <10% in 2005–2007).

Adult females and males were captured during the nesting period by hand or using one of two prop-trap methods (Stutchbury and Robertson 1986, Friedman et al. 2008). We determined age class of females by differences in plumage, which is readily distinguishable between second year (SY) and after second year (ASY) birds (Robertson et al. 1992). One primary feather (P1) was removed from each wing, and 100 µl of blood was drawn from each individual as part of a different study on mercury contamination. We banded nestlings three to five days before fledging. After the first brood of Tree Swallows in a nest box had fledged, we attempted to remove the old nests within one week. Tree Swallows that subsequently laid eggs in those nest boxes were captured and monitored as potential double-brooded birds. We confirmed double-brooding by a female by capturing her and noting her USGS band number. Birds initiating late nests in nest boxes that had not contained successful Tree Swallow nests were monitored identically. Females with failed first clutches were followed through any later nests but were not considered double brooded.

During each breeding season, nest initiations occurred in two discrete time periods. The majority of nests was initiated in late April or early May (hereafter, early breeding round), with a second wave occurring in late May and June (i.e., late breeding round). In each season, we defined the end of the early breeding round as the first period of more than two days without a new nest initiated. Because we did not capture or disturb females during incubation, females that abandoned unhatched eggs (n = 8 in 2006, n = 14 in 2007) could have been unbanded, and if they attempted to renest, we would have misclassified them as late nesters.

STATISTICAL ANALYSES

We defined productivity for first or second broods as the number of chicks alive on the last visit before fledging (nestling day 14–16), minus any dead nestlings found after fledging. Productivity of single- and double-brooded birds was compared using a two-tailed t-test. In order to examine factors influencing the probability of double brooding, we performed a binary logistic regression using MINITAB Statistical Software Version 15, (Minitab Inc., State College, Pennsylvania), with double brooding as the response variable, and female age class, clutch initiation date, clutch size, wing length, and weight as predictors. For all analyses, we established $\alpha = 0.05$ as our significance level, and all means are presented ± SD.

RESULTS

FREQUENCY OF DOUBLE BROODING

Among all females nesting in the early breeding rounds of 2006 and 2007, 5% of birds with successful first clutches (16 of 301) later laid second clutches. During the 2005 pilot study, both of the double-brooded females initiated their first clutches before the median (hereafter, peak) of clutch initiation, so we examined early-nesting females separately in 2006–2007. Of all females that initiated clutches before peak of clutch initiation each year, 15% raised second broods (19% in 2006, 11% in 2007; Fig. 1).

In 2006, 25% of females nesting in the late breeding round (nine of 36) were raising their second broods. In 2007, 21% of late-nesting females (seven of 34) were double brooded. We caught nearly every female that hatched eggs in our boxes in 2006–2007 (99%; 422 of 427), so it is unlikely that we missed any double-brooded birds.

In 2006, the first five females to nest in the early breeding round were all eventually double brooded, as were the first two females to nest in 2007 (Fig. 1). In both years, the majority of double-brooded females initiated their first clutches before the peak of clutch initiation (range: 18–30 April 2006, 28 April–6 May 2007; Fig. 1). Second clutches were laid from 7–19 June in 2006 and 12–26 June in 2007. Standardizing each season so that the first clutch was initiated on the same day, double-brooded females initiated their first clutches 5.4 ± 3.0 days after the first egg of the season (n = 16), while single-brooded females waited 12.8 ± 6.9 days (n = 284). Double-brooding females waited, on average, 9.3 ± 3.2 days after young from their first nest had fledged before initiating a second clutch (range: 3–15 days).

Using logistic regression, we tested the effects of female age class, wing length, and weight, as well as the size of the first clutch and its date of initiation, on likelihood of double brooding. The overall model was significant (log-likelihood = –45.8, df = 5, $P < 0.001$), with both clutch initiation date and clutch size yielding significant negative effects, such that females with earlier and smaller clutches were more likely to breed twice within a season (coefficient ± SE: clutch initiation date = –0.31 ± 0.08, $P < 0.001$; clutch size = –0.75 ± 0.37, $P = 0.05$; age class = 0.24 ± 0.85, $P = 0.78$; mass = 0.12 ± 0.20, $P = 0.55$; wing length = –0.05 ± 0.12, $P = 0.67$).

FIDELITY TO NEST BOXES AND MATES BETWEEN CLUTCHES

Across all three years, 14 out of 18 females raised their second broods in the same nest boxes as the first (Table 1). One female was double-brooded in both 2005 and 2006 and used the same box for all four nests. We caught only five of the males paired with double-brooded females in the late breeding rounds of the three years combined, and four (80%) of those were the same males that the females had been paired with during their first clutches of that year (Table 1). Over the three years combined, nine second broods were in mercury-contaminated sites, and nine were in reference sites. Because nest boxes were distributed approximately equally across contaminated and reference sites, this indicates that double-brooding behavior was not related to mercury contamination.

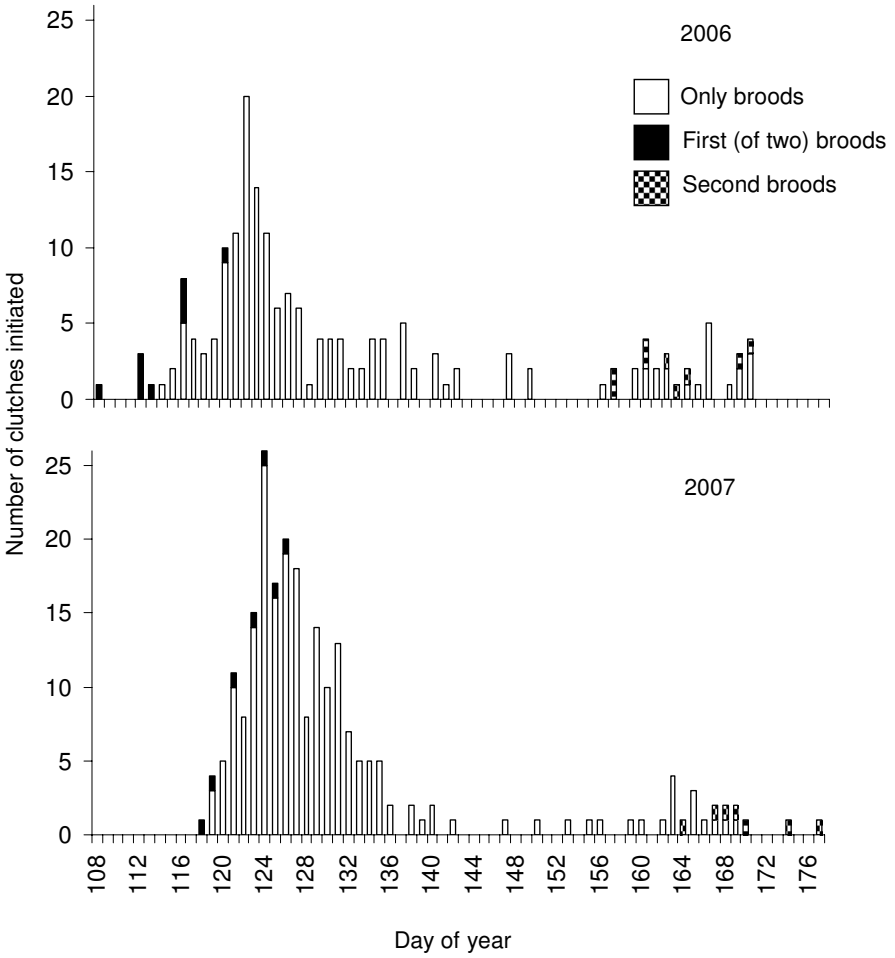

FIGURE 1. The number of nests initiated each day by Tree Swallows between 18 April and 26 June during the breeding seasons of 2006–2007 in the Shenandoah Valley, Virginia (day of year: 108–177).

PRODUCTIVITY OF DOUBLE-BROODED FEMALES

On average, double-brooded swallows ($n = 16$) laid 5.7 ± 0.7 eggs in their first nests and 4.4 ± 0.6 eggs in their second nests. By way of comparison, females nesting only in the early breeding rounds produced 5.9 ± 0.9 eggs ($n = 285$), while those nesting only in the late breeding rounds laid clutches of 4.3 ± 0.9 eggs ($n = 48$). Productivity for double-brooded females for 2006–2007 was 4.4 ± 1.3 fledglings from first clutches and 3.4 ± 0.8 from second, for total productivity of 7.7 ± 1.5. Swallows that nested only in the early breeding rounds produced 4.7 ± 1.5 fledglings ($n = 285$ successful nests, 2006–2007 combined). Thus, double-brooded females significantly increased their total annual productivity compared to birds nesting only in the early rounds of breeding ($t_{17} = 7.3$, $P < 0.001$, 2006–2007 combined).

DISCUSSION

Double brooding has been reported only occasionally in the well-studied Tree Swallow, but little is known about why it occurs or its consequences. We performed an opportunistic study of double-brooded Tree Swallows in the southern portion of their contiguous breeding range. Approximately 5% of females that had successful first clutches raised two broods in a single season. These tended to be the earliest nesting females, such that 15% of females initiating successful first nests before the median date of clutch initiation later initiated second clutches. During the late breeding round, approximately a quarter of the females were raising their second broods on our study site, the remainder either being late breeders or possibly having moved in after nesting elsewhere. Females that initiated second clutches were not older, larger, or heavier than those that did not, but they had produced smaller first clutches. This suggests the possibility that females had already made the behavioral decision to double brood when laying their first clutches. However, the effect of clutch size was statistically marginal, so further study is necessary to determine whether double-brooded females generally have smaller first clutches. What is clear is that nesting early strongly predicted double brooding.

Double brooding markedly increased annual productivity by nearly doubling the number of fledglings produced by a female in one breeding season. In contrast with what is normally reported for this well-studied species (Robertson et al. 1992, Hussell 1983, 2003a), our results from the southern portion of the breeding range suggest that double brooding in Tree Swallows, while not ubiquitous, occurs regularly.

TABLE 1. Clutch size and number of fledglings produced in each clutch for double-brooded Tree Swallow females breeding in Augusta and Rockingham counties, Virginia, from 2005–2007. C and R represent contaminated and reference sites with respect to a larger study on mercury contamination. NC indicates males that were not captured.

					Clutch size		Fledglings produced	
Band	Year	C or R	Age	Mate	First	Second	First	Second
182171015	2005	R	SY	NC	5	5	5	5
182171029	2005	C	SY	NC	4	3	3	3
182171015	2006	R	ASY	NC	6	5	6	4
182171023	2006	C	ASY	NC	7	5	6	2
182171334	2006	R	ASY	Same	6	3	5	3
192105501	2006	C	ASY	NC	5	5	5	2
192105503	2006	R	ASY	Same	5	4	4	4
192105505	2006	R	SY	NC	5	5	3	4
192105508	2006	R	ASY	Same	5	4	5	4
192105509	2006	C	ASY	New	5	4	4	4
192105513	2006	C	SY	Same	6	5	1	3
192104432	2007	R	ASY	NC	6	4	5	3
192104469	2007	R	SY	NC	6	4	4	4
182171293	2007	R	ASY	NC	5	4	4	2
192104423	2007	C	ASY	NC	7	4	6	4
192105453	2007	C	ASY	NC	6	5	3	3
182171020	2007	C	ASY	NC	6	5	4	4
192105545	2007	C	ASY	NC	5	5	5	4

Several factors can favor double brooding. An increase in food abundance could prompt birds to raise second broods (Gavin 1984, Moore and Morris 2005, Nagy and Holmes 2005). We do not believe this occurred during our study. In fact, the first breeding round in 2006 occurred during an uncharacteristic period of drought that is unlikely to have increased food abundance. Blancher and Robertson (1982) suggest that a reduction in post-fledging care by a pair of Eastern Kingbirds (*Tyrannus tyrannus*) permitted time to breed twice, and others have proposed a trade-off between investment in the first brood and the second brood (Verboven et al. 2001). Tree Swallows typically care for their offspring for at least three days after fledging (Robertson et al. 1992), though we have no data on the parental care provided by our double-brooded females. The interclutch interval of nine days suggests that double brooding may not preclude typical duration of parental care.

Of double-brooded Tree Swallows in Ontario, Hussell (1983) suggested that, in years with longer breeding seasons, swallows have more time to raise second broods. All double-brooded swallows in our population were among the earliest-nesting birds, and this was the most important predictor in our logistic regression. Thus, availability of time may explain why these individuals nested twice (Kloskowski 2001). These early-nesting females could have been in better condition than single-brooded females, as Rooneem and Robertson (1997) suggest condition affects the likelihood of relaying after predation in this species; however, we found no evidence that double-brooded birds were heavier, larger, or older than single-brooded ones.

Our study site is located near the southern border of the Tree Swallows' contiguous breeding range (Sauer et al. 2005), and thus their breeding season begins earlier than those nesting further north. In 2006, the first breeding round at our study site was early—apparently the earliest Tree Swallow nest initiation ever recorded in Virginia (R. Clapp, U.S. Geological Survey, pers. comm.). In 2007, the first clutch was initiated 10 days later than in 2006, but 4% of the birds overall and 11% of females nesting before median clutch initiation still raised two broods. Thus, the phenomenon of double brooding is not restricted to years with unusually early breeding. The only report of comparable levels of double brooding in this species comes from another southerly site with a protracted and early breeding season. At that site, in southern California, 17 females laid second clutches at a site with 111 nest boxes over the course of three years (Wasserman 2003). It is probably not a coincidence that these two examples of regular double brooding come from the southern portion of the breeding range, as southerly breeding Tree Swallows can start nesting earlier than those to the north, but it remains to be confirmed that double brooding is not occurring at sites to the north as well. With the exception of those at Long Point, Ontario, (Hussell 1983, 2003a), most studies of Tree Swallows have not reported whether nests were checked after fledging of the first brood. Thus, double brooding may already be occurring throughout the range but be underappreciated. In our study, we not only checked all nest boxes after fledging but also cleaned out the first nests whenever possible. Nest removal may have encouraged reuse of nest boxes but was not necessary for it to occur, as females often laid new clutches on old nests before we were able to remove them. Further studies in which all females are banded during the early round, nest boxes are rechecked 2–3 weeks after fledging, and old nest contents are handled systematically will be required to determine the incidence of double brooding within the central and northern portions of the species' range.

In general, late summer and fall nesting among North American birds is underappreciated and may be increasing due to global warming (Koenig and Stahl 2007). There is disagreement in the literature concerning whether Tree Swallows have started responding to climate change by nesting earlier (Dunn and Winkler 1999, Hussell 2003b). The double-brooding behavior reported here may become more common if Tree Swallows are in fact nesting earlier than in the past. In addition, more Tree Swallows may be nesting in the southern portion of their typical range; they have recently been documented nesting as far south

as South Carolina (Wagner et al. 2002). Because Tree Swallows have become a widely used model species for life history studies and ecotoxicological monitoring, both of which can require assessment of annual reproductive output, it is imperative that the Tree Swallow be recognized as a species that can potentially double its reproductive success through double brooding.

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