




Nest feathering responses by Tree Swallows (*Tachycineta bicolor*) to experimental warming

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Abstract

Among many functions, bird nests protect eggs, developing young, and incubating adults from inclement weather. In Tree Swallows (*Tachycineta bicolor*), prior to and while females are incubating, males compete with rivals for feathers that they use to line nests. The thermal benefits hypothesis proposes that males add feathers to improve heat retention of nests. We tested this hypothesis on Tree Swallows nesting near Wolfville, Nova Scotia, Canada in 2013, 2014, and 2015, and in St. Denis, Saskatchewan in 2013. In 2013, at both locations we experimentally heated nests. After young had fledged, we counted and measured feathers in each nest. The hypothesis was not supported. The only significant result was that St. Denis (52.2°N) had fewer feathers than the Annapolis Valley (45.1°N) site, which is contrary to expectation. Our findings challenge the prevailing hypothesis for why male Tree Swallows feather nests.

Keywords Artificial heating · Thermal benefits hypothesis · Nest heat retention · Nest microclimate

Zusammenfassung

Die Ausstattung des Nestes mit Federn als Reaktion auf experimentelle Erwärmung bei Sumpfschwalben (*Tachycineta bicolor*)

Neben vielen anderen Funktionen schützen Vogelnester Gelege und die sich entwickelnden Küken sowie die brütenden Altvögel vor schlechten Witterungsbedingungen. Vor und während der Bebrütung durch die Weibchen konkurrieren die Männchen der Sumpfschwalben (*Tachycineta bicolor*) mit Rivalen um Federn, die sie zur Auskleidung ihrer Nester benutzen. Nach der Thermal Benefits-Hypothese fügen Männchen den Nestern Federn hinzu, um das Wärmerückhaltevermögen der Nester zu verbessern. Wir testeten diese Hypothese an brütenden Sumpfschwalben nahe Wolfville, Nova Scotia, Kanada, in den Jahren 2013, 2014, 2015 und in St. Denis, Saskatchewan, Kanada, in 2013. In 2013 erwärmten wir in beiden Untersuchungsgebieten die Nester. Nach dem Ausfliegen der Jungen haben wir in jedem Nest die Federn gezählt und sie vermessen. Die Hypothese wurde nicht gestützt. Das einzige signifikante Ergebnis war, dass die Nester in St. Denis (52.2°N) weniger Federn hatten als in dem Gebiet im Annapolis Valley (45.1°N), was der Erwartung widersprach. Unsere Ergebnisse stellen die vorherrschende Hypothese in Frage, warum Sumpfschwalben Männchen ihre Nester mit Federn ausstatten.

Introduction

Bird nests protect eggs, nestlings, and incubating adults from predation and inclement weather (Welty 1982). Cavity nests in particular can provide shelter from predators and reduce

negative effects of rain, wind, and excessive cold or heat (Lack 1954; Nice 1957; Collias and Collias 1984). Suitable microclimates in nests are essential to a breeding bird's fitness, because maintenance of proper egg temperatures is critical for development of avian embryos, as well as for energy conservation by incubating birds (White and Kinney 1974; Olson et al. 2006; Bicudo et al. 2010). Accordingly, many bird species line their nests with soft insulatory materials such as fine grasses, plant down, lichens, and mosses, although mammal fur and feathers likely provide the best insulation (Collias and Collias 1984; Bicudo et al. 2010). In addition, many cavity-nesting birds choose sites with

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entrances on leeward sides of trees that offer protection from inclement weather (Facemire et al. 1990), or with entrances that face south to increase solar insolation (Austin 1974; Ardia et al. 2006).

In Tree Swallows (*Tachycineta bicolor*), females do most of the nest-building (Austin and Low 1932; Bent 1963; Sheppard 1977; Lombardo et al. 1995; Sibley 2001); however, it is predominantly males that participate in aerial battles for feathers with which to line nest cups (Bent 1963; Sheppard 1977; Ringelman 2007). Feathers preferred by swallows are often large, light colored, and have a large portion of down at their bases (Forbush 1929; Bent 1963; Sheppard 1977; Tufts 1986). A variety of feathers from a large number of taxa may be used (Austin and Low 1932; Bent 1963). There are several hypotheses for why males collect feathers for lining their nests (Winkler 1993; Scarazzini 1999; Maderson 2003; Jensen-Jarolim 2013); we focus here on the thermal benefits hypothesis (White and Kinney 1974; also see “Appendix 1”).

The thermal benefits hypothesis makes several predictions. The first is that male Tree Swallows add feathers to nests to improve heat retention (White and Kinney 1974; Olson et al. 2006). In support of this prediction, nestlings in better feathered nests were heavier and larger (wing chord and tarsus) at 12 days of age and fledged earlier than nestlings in less feathered nests (Winkler 1993). Similarly, Great Tits (*Parus major*) in Spain had higher hatching success if their nests had more insulatory materials (Álvarez et al. 2013). Also, Reid et al. (2000) recorded more fledglings per egg in heated European Starling (*Sturnus vulgaris*) nests in comparison to controls.

A second prediction of the thermal benefits hypothesis is that nests will have more, or a higher volume of, feathers at higher, colder latitudes (Winkler 1993; McGowan et al. 2004). Although no studies have previously tested this in Tree Swallows, in Blue Tits (*Cyanistes caeruleus*) and Great Tits, females breeding at higher latitudes added more insulatory material (Mainwaring et al. 2012).

A third prediction of the thermal benefits hypothesis is that nests built early in the season will have more insulation because of lower ambient temperatures (Lombardo 1994; Britt and Deeming 2011). In support of this, Deeming et al. (2012) found that temperatures experienced by Great and Blue Tits, irrespective of latitude, affected insulatory properties of nests. Although Lombardo (1994) found no support for this prediction in Tree Swallows, Liljesthrom et al. (2009) did in Chilean Swallows (*Tachycineta meyeni*). Liljesthrom et al. (2009) noted that Chilean Swallows nest in colder climates (mean daily ambient temperature during the breeding season ~ 9 °C) than Tree Swallows (~ 17 °C; Winkler 1993) and add six times as many feathers as Tree Swallows, suggesting that the former conditions select more strongly for feathering.

We experimentally tested the thermal benefits hypothesis on Tree Swallows breeding in Canada. Although previous studies have tested if the presence or absence of feathers affected chick development (Lombardo et al. 1995), no study that we are aware of has determined if adult Tree Swallows regulated numbers of feathers in response to internal box temperature. If feathers are added primarily for insulation, one would expect that warmer nests would require less feathering. Therefore, we predicted that if we artificially raised temperatures within boxes, males would add fewer feathers. We also tested if box size influenced feathering, because we assumed that smaller boxes would require fewer feathers to provide adequate insulation, in comparison to larger volume boxes. Ambient temperature generally decreases at higher latitudes and increases over the course of the breeding season. We also evaluated latitudinal and seasonal differences in number and length of feathers added by Tree Swallow breeding at two locations in Canada.

Materials and methods

Nova Scotia

Tree Swallows using wooden nest boxes adjacent to orchards were studied from May to July 2013–2015 in the Annapolis Valley, Nova Scotia (NS), Canada ($45^{\circ}5'52''\text{N}$, $64^{\circ}24'34''\text{W}$ and $45^{\circ}6'9''\text{N}$, $64^{\circ}18'18''\text{W}$) (additional details in Hainstock et al. 2010; Shutler et al. 2012). Boxes were ~ 1.5 m above the ground on metal poles ≥ 25 m from neighboring boxes (Muldal et al. 1985). Small boxes ($n=80$, 80, and 76 for 2013, 2014, and 2015, respectively) had a volume of 7000 cm^3 and a 3.8-cm-diameter entrance hole, and large boxes had a volume of $12,000\text{ cm}^3$ and either a 3.8- ($n=42$, 42, 53) or 5.3-cm-diameter ($n=19$, 19, 15) entrance hole (MacCulloch 2004). In 2015, an additional box size was added ($n=45$), with a total volume of 5323 cm^3 and a 3.8-cm opening; these latter boxes were pooled with the other small boxes without qualitatively changing results.

Most females were captured opportunistically in boxes during incubation (Custer et al. 2007; Betini and Norris 2012). Captures at this time may have been associated with some abandonment (e.g., Burt and Tuttle 1983; Cohen 1985), but, as part of a larger study, were essential for identifying females that may have nests depredated early in breeding. Traps inside boxes (Magnusson 1984; Yunick 1990) were also used to capture adults when nestlings were ~ 4 days old. Females were aged and sexed based on plumage characteristics as second year or after second year (Sheppard 1977; Hussell 1983; Lombardo et al. 1995).

In 2013, wire mesh platforms were added under nests at day 2 or 3 of nest-building so that heating pads (large Heat Factory 24-h oxidizing warmers; Heat Factory, Vista,

CA) could be inserted with minimum disturbance to nests and eggs (Dawson et al. 2005; Fast 2007). At this stage, warmers were placed under platforms below nesting material. Warmers were guaranteed to provide heat for 24 h, although most were still emitting heat the subsequent day. We randomly assigned nests to a control or heat treatment (nest box size was not considered at this stage). Nests were then paired by initial numbers of feathers (determined visually) lining them ($n = 68$, mean \pm SD number of feathers 3 ± 5.6), so that starting conditions were roughly similar. Heated nests had heating pads replaced daily (between 22 and 27 May, new warmers were not used because of a delay in shipment; nonetheless, all nests were still visited daily) until culmination of the incubation period (~14 days). We added previously oxidized pads to control nests to equalize disturbance. We visited nests daily to replace warmers, as well as to determine dates that first eggs were laid, date that first nestlings hatched, number of eggs hatched, and number of nestlings fledged (number of nestlings banded at day 12 post-hatch, minus any dead found in boxes on day 22). Heating manipulations stopped once the first nestling hatched because Tree Swallows rarely add feathers to their nests when they are feeding nestlings (Winkler 1993). As an additional metric of feathering, we measured each feather's length and width. Feather width was discarded as a variable because feces matted many feathers so that original width could not be reliably measured.

In 2013, once we had begun using warmers, we collected temperature data from within a few boxes with Watch-Dog data loggers. Loggers were externally attached to the opposite side of nest entrances to reduce potential neophobic responses by nesting adults. A small thermo-sensitive probe attached to loggers was buried in nesting materials under centers of nest cups. Four data loggers were used, two of which we deployed in control boxes, and two of which we deployed in heated boxes. Active boxes were randomly selected, and data loggers deployed for 23–72 h, after which they were switched to different boxes. Previous studies on Tree Swallows showed that heating pads raised nest box temperatures by an average of 5.6 °C over ambient temperatures (Dawson et al. 2005; Fast 2007). Ambient temperature data were collected from the nearest Environment Canada monitoring site at the Kentville Research Centre, 13 km west of Wolfville (Environment Canada 2013).

We distinguish nesting initiation date as when boxes had adults present or nesting material lining boxes, and clutch initiation date as when a first egg was laid. Nest fates were categorized as in “Appendix 2”. We only analyzed feathers from nests in which nestlings fledged; otherwise nest feathering may not have been complete. Fledged nests were scraped out of boxes into individual bags and returned to our lab. All feathers were separated from nesting material by hand, counted, and measured flattened to the nearest

millimeter using a ruler. To ensure consistency, all measurements were taken by the first author.

Saskatchewan

In 2013, feathers from 18 nests (nine heated and nine controls) were obtained from a heating experiment from the St. Denis National Wildlife Area (52°8'49"N, 106°9'56"W), east of Saskatoon, Saskatchewan (SK). In this case, heating began shortly after nestlings hatched and was for a different experiment to test for effects on corticosterone, but other methods were the same as those in Nova Scotia. Ambient temperature data were collected from the nearest Environment Canada monitoring site at the Saskatoon International Airport in Saskatoon, Saskatchewan, 46.3 km west of St. Denis (Environment Canada 2013).

Analyses

Data were analyzed in SAS 9.4 (SAS Institute, Cary, NC). Values are reported as mean \pm SD. We counted number of feathers and averaged feather lengths for each nest. For Nova Scotia, we used a general linear model (GLM) to test whether number of feathers and feather lengths were related to year, and a separate GLM to test whether numbers of feathers and feather lengths were related to box size. For 2013, we used a GLM to test whether numbers of feathers and feather lengths were related to heat treatment and latitude (St. Denis vs. Wolfville).

Results

General observations

Temperature loggers were deployed in a total of 13 boxes; data from two boxes were excluded because of recorder failure (loggers did not record temperatures, or temperatures recorded were > 200 °C). For remaining deployments, control boxes ($n = 4$) had lower internal temperatures than heated boxes ($n = 7$; mean difference in temperature $+ 3 \pm 3$ °C). Although this difference in temperature was not statistically significant (ANOVA, $F_{1,9} = 2.8$, $P = 0.13$), samples were small. Moreover, successful heating using these pads has been demonstrated elsewhere (Dawson et al. 2005; Fast 2007).

Of Nova Scotia nests initiated, 21 of 68 in 2013 (number of feathers 87.7 ± 28.2 ; feather length 8.4 ± 1.0 cm), 22 of 43 in 2014 (number of feathers 90.5 ± 53.2 ; feather length 8.4 ± 1.2 cm), and 19 of 35 in 2015 (number of feathers 73.9 ± 32.1 ; feather length 8.0 ± 1.1 cm) produced fledglings (“Appendix 2”). From fledged nests, we measured lengths of 5270 feathers (2013, 1830; 2014, 2576; 2015, 1360), with

almost all nests containing duck (*Anas* spp., 60/62; 97%) and gull (*Larus* spp., 58/62; 94%) contour feathers (feathers from 11 other species were present in fewer than 47% of nests). Number of feathers per nest (hereafter “feather number”; $R^2=0.03$, $F_{2,58}=0.8$, $P=0.46$) and feather length ($R^2=0.04$, $F_{2,58}=1.2$, $P=0.30$) in Nova Scotia were similar among years. Therefore, years were pooled in some analyses of feathering. For Nova Scotia, there was no statistically significant difference in feather numbers relative to box volume (pooling data from 2013 to 2015; $n=41$ small and 23 large boxes; $R^2<0.01$, $F_{1,59}<0.1$, $P=0.91$). However, and contrary to our expectation, smaller boxes had larger feathers ($R^2=0.11$, $F_{1,58}=7.0$, $P=0.01$).

Thermal benefits hypothesis

In 2013, the 6-day break in addition of warmers resulted in eight control and seven heated nests not being manipulated. Regardless, there was no significant difference in feather number between control (88.5 ± 23.5) and heated (86.3 ± 34.5) nests that were not treated at this time, and control ($n=5$; 82.0 ± 23.0) and heated ($n=1$; total feathers 59) nests that experienced no break in treatment (ANOVA; $F_{3,17}=0.5$, $P=0.67$). There was likewise no significant difference in feather length between control (8.2 ± 2.8) and heated (8.3 ± 2.5) nests that were not treated at this time, and control (8.6 ± 2.5) and heated (9.1 ± 2.5) nests with no break in treatment (ANOVA; $F_{3,17}=0.2$, $P=0.91$). Overall, there was no statistically significant difference in feather numbers (control 86.0 ± 23.5 , range 47–148; heated 89.8 ± 32.7 , range 47–157) or lengths (control 8.39 ± 2.7 ; heated 8.39 ± 2.5) between control and heated nests (Table 1; Fig. 1), or in feather lengths at the two latitudes (NS 8.4 ± 2.6 ; SK 8.3 ± 2.5). However, and contrary to the hypothesis, fewer feathers were added to nests at the higher latitude site (NS

Table 1 Results of general linear model (GLM) tests of the thermal benefits hypothesis where heat treatment involved experimentally warming nests and latitude was compared between a site near Saskatoon, Saskatchewan and in the Annapolis Valley of Nova Scotia, Canada

Response variable	Explanatory variable	df	R^2	F	P
Feather number	Heat treatment	1,26		0.2	0.65
	Latitude	1,26		11.9	0.002
	Overall model	2,26	0.32	6.1	0.007
Feather length	Heat treatment	1,26		< 0.1	0.98
	Latitude	1,26		0.1	0.79
	Overall model	2,26	< 0.01	< 0.1	0.96

For feather number, the association with latitude remained significant with removal of heat treatment, and for feather length, no significant association emerged if heat treatment was dropped from the model (Crawley 2005)

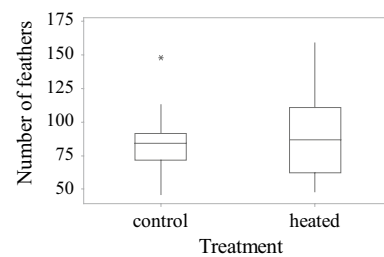


Fig. 1 There was no significant difference in feather number between control and heated nests

87.7 ± 27.5 ; SK 54.4 ± 15.9 ; Table 1; Fig. 2). In addition, relationships between clutch initiation date and feathering ($R^2=-0.23$, $P=0.31$) and clutch initiation date and feather length ($R^2=-0.02$, $P=0.91$) were not significant.

Discussion

We found no support for the thermal benefits hypothesis, that feather addition in Tree Swallows would be facultative in response to interior box temperature. In fact, control boxes had slightly more feathers on average than heated boxes. Moreover, our only significant finding was that a higher latitude site had fewer feathers, which is contrary to expectation. The interval when we did not heat boxes may have reduced the difference between control and heated boxes, but differences in both feather number and lengths between boxes that were not heated during this time, and boxes where heating was uninterrupted, did not even approach significance. If feather addition was facultative in response to box temperature, we should have observed at least a suggestive increment in feathering in control boxes.

Contrary to the thermal benefits hypothesis, Nova Scotia nests had significantly more feathers than did Saskatchewan nests, despite St. Denis being 780 km north of Wolfville. This outcome could be related to spatial variability in feather availability or to temperatures in 2013. Historically in May, Nova Scotia temperatures are 2.2 °C lower to 0.3 °C higher

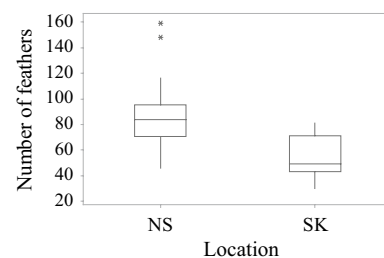


Fig. 2 Tree Swallows added more feathers to nests at the lower latitude Nova Scotia (NS) site than at the higher latitude Saskatchewan (SK) site

than those in Saskatchewan, and in June temperatures in Nova Scotia are 1 °C lower to 0.9 °C higher than those in Saskatchewan. This year, during the initial week of the season (1–7 May), ambient temperatures in Nova Scotia were only 0.1 °C higher than those in Saskatchewan. From 22 to 28 May, temperatures in Nova Scotia were 1.4 °C lower than those in Saskatchewan (Environment Canada 2013). Cooler temperatures often lead birds to increase amounts of insulatory materials in their nests (Rohwer and Law 2010; Britt and Deeming 2011; Mainwaring et al. 2012). However, daily average temperatures for 2013 were comparable to daily averages from 1981 to 2010 in both the Nova Scotia and Saskatchewan sites (unpublished data). There was also a non-significant negative relationship between clutch initiation date and feathering, but this could have been due to the lower quality of later paired males (Lozano et al. 1996).

Future research should compare insulative materials other than number and length of feathers. Although downy feathers have higher insulative properties than vegetable matter (Reid et al. 2002; Hilton et al. 2004), Tree Swallow nests are primarily constructed of dried grasses (Lombardo et al. 1995), which could significantly contribute to heat retention. Nests with more vegetable material may therefore require fewer feathers. Alternately, a smaller box could be associated with increased heat retention (Wiebe and Swift 2001), which could in part be associated with a higher density of nesting material.

Not only could relative ambient temperature and feather availability affect feather numbers, genetic differences between Nova Scotia and Saskatchewan populations could also be important. Our tests assumed facultative responses to thermal treatments, but feathering may be genetically programmed. Tree Swallows do have latitudinal variation in immune responses across their range (Ardia 2007) and swallow species living at higher latitudes have larger mean clutch sizes and faster growth rates than their counterparts at lower latitudes (Dunn et al. 2000; McCarty 2001). These data suggest latitudinal selection for different reproductive strategies that may have a genetic component. However, latitudinal variation in clutch size could occur because risk of hyperthermia is greater in nests with larger broods, and typical temperatures at lower latitudes could affect this risk (Royama 1969; Mertens 1977). Moreover, there is substantial mingling of Tree Swallow populations (Knight et al. 2018), which likely reduces genetic structuring of populations. Therefore, latitudinal ambient temperature and day length may determine clutch size, and both ambient temperature and clutch size may affect nest feathering by male swallows.

In summary, we found no evidence that feather addition was facultative in response to box temperature, box size, female age, or clutch initiation date. Other variables may also influence feather addition, and other hypotheses [“Appendix 1”, anti-abrasion, because nestlings lack

a protective feather layer of their own (Scarazzini 1999; Maderson 2003; Jensen-Jarolim 2013) and anti-ectoparasite (Winkler 1993)] may warrant testing. Further studies are needed to determine if feather number and length in Tree Swallow nests is facultative in response to combinations of these variables. Finally, we note that if feathers are so important, then why are there so few species that make use of them in lining their nests?

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Compliance with ethical standards

This study complies with the current laws of Canada. All applicable institutional guidelines for the use of animals were followed, with both the Acadia Animal Care Committee and the University of Saskatchewan Animal Care Committees having approved all research. All procedures performed were in accordance with the ethical standards of the institution at which the studies were conducted.

Conflict of interest The authors declare that they have no competing interests.

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Appendix 1: The recruitment probability hypothesis

The recruitment probability hypothesis proposes that males add more feathers to nests they judge to be of higher value (metrics described in Hainstock et al. 2010). Broods of such nests may be associated with higher quality females that invest more in individual eggs, that lay larger clutches, or that have more breeding experience raising clutches (Stutchbury and Robertson 1988), and males may add extra feathers to signal to females their future paternal care, or for heat retention (but see above). Progeny produced by these females are assumed to have a greater potential to contribute to a male’s Darwinian fitness. Males may assess female quality based on her age class, which in Tree Swallows can be evaluated using plumage characteristics, clutch initiation date [date that a first egg is laid, which is earlier for older

females (Stutchbury and Robertson 1988) and is strongly associated with recruitment (Shutler et al. 2006), and clutch size [which is strongly associated with lifetime reproductive success (Shutler et al. 2006)]. Although in Lesser Black-backed Gulls (*Larus fuscus*), larger clutch size is associated with lower quality eggs (Nager et al. 2000), in three tit species (Blue, Great, and Coal tits, *Parus ater*), clutch size determination of females is based on their own ability to feed their young and has nothing to do with mate quality, with lower quality females producing smaller clutches (Slagsvold and Lifjeld 1990). We are unaware of a study that has assessed whether brood value influences feathering.

In Nova Scotia in 2014, trios of nests initiated on the same day were randomly assigned to reduction (two eggs removed), control (two eggs picked up and replaced), or addition (two eggs added) treatments. Eggs from reduce clutches were placed in addition clutches. Modal clutch size in this population was five. We predicted that if we experimentally decreased and increased clutch size that males would add fewer and more feathers, respectively, because of changes in brood value. Similarly, we predicted that males would add fewer feathers to nests of younger females.

Table 2 Results of GLM tests of the female quality hypothesis

Response variable	Explanatory variable	df	R ²	F	P
Feather number	Female age	1.56		1.9	0.17
	Clutch initiation date	1.56		0.1	0.78
	Clutch size	1.56		0.1	0.82
	Overall model	3.56	0.04	0.7	0.57
Feather length	Female age	1.56		0.3	0.63
	Clutch initiation date	1.56		< 0.1	0.94
	Clutch size	1.56		0.6	0.44
	Overall model	3.56	0.02	0.3	0.82

Excluding nests where clutch sizes were manipulated did not qualitatively change results, and no significant associations were obtained with sequential removal of the least significant variables (Crawley 2005)

Table 3 Success rates and treatments for Tree Swallow (*Tachycineta bicolor*) nests initiated in the Annapolis Valley, Nova Scotia, 2013–2015

	2013 (n=67)		2014 (n=44)		2015 (n=36)		
	Control (n=36)	Heated (n=31)	Addition (n=5)	Subtraction (n=6)	Control (n=4)	No treatment (n=29)	No treatment
Abandoned	17	12	0	0	0	0	1
Abandoned with eggs	1	4	0	1	0	11	11
Depredated with eggs	2	5	0	1	0	3	4
Abandoned with nestlings	2	1	0	0	0	0	0
Depredated with nestlings	1	1	0	1	0	4	1
Fledged	13	8	5	3	4	11	19

Abandoned No eggs were laid and nest was abandoned, *Abandoned with eggs* at least one egg was laid in nest, *Depredated with eggs* nest abandoned with nestlings (at least one egg hatched), *Fledged* nests from which at least one nestling fledged

We used a GLM to test whether number of feathers and feather lengths were related to female age, clutch initiation date, and clutch size. Only 22 nests fledged from the clutch manipulation experiment, so that statistical comparisons among treatments had little power. Therefore, we simply considered feather number and feather lengths simultaneously for both manipulated and non-manipulated nests from all 3 years. Female age, clutch initiation date, and clutch size were not associated with feathering (Table 2). Results were qualitatively similar when experimental clutch manipulations were excluded.

We therefore found no support for the recruitment probability hypothesis, although our experimental power was low, with only eight of 11 manipulated nests successfully fledging. It is also possible that males may assess recruitment probability through metrics other than those we tested. Female Tree Swallows select males that have brighter plumage for extrapair copulations (Bitton et al. 2007) and it is possible that males use plumage brightness to assess female quality and hence brood value. Although we found no correlation between female age and number or length of feathers added by males, we did not evaluate plumage brightness within age classes. The mating system of Tree Swallows may also weaken selection for males to impress partners with feathering. First, Tree Swallows have one of the highest documented rates of extra-pair paternity in birds (Dunn et al. 1994). Second, Tree Swallows over most of their range have only a single clutch per year, and in fewer than 18% of cases do the same adults pair in successive years (Shutler and Clark 2003; Shutler et al. 2006; Winkler et al. 2011). In any case, our tests should be replicated with larger samples.

Appendix 2

See Table 3.

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