Aerial competition for feathers by Tree Swallows (*Tachycineta bicolor)*

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Undergraduate Honors Thesis

Abstract

During the breeding season, Tree Swallows (*Tachycineta bicolor*) scavenge for feathers and use them to line their nests. Nest lining is known to be an important factor in Tree Swallow reproductive success, but competition for feathers has never been experimentally studied despite the fact that acrobatic aerial competitions for feathers are frequent and easily observable. To examine the proximate and ultimate causes of feather contests, I manipulated the nest-lining of breeding swallows and then observed individual behaviors throughout the breeding season. Both males and females gathered feathers, beginning with nest construction and continuing through chick rearing. It is clear that there are two distinct methods of feather gathering: feather "collection," an early-season behavior characterized by a lack of interaction with other birds, and feather "contests," conspicuous, aggressive interactions involving several birds. Contests over larger feathers were more intense than those over smaller feathers. Early-season contest winners tended to exhibit drop-catch displays with the feather, had well-feathered nests, and were ultimately reproductively successful; there is some evidence that these contest winners may be higher quality individuals. The number of feathers in the nest at the time of a contest was also an important determinant of behavior. A late-season individual with a well-feathered nest tended to participate less in contests and drop the feather more frequently. The associations and feedbacks among contest performance, individual quality, the number of feathers in the nest, and reproductive success indicate that feather contests involve complex behaviors that are highly variable among individuals and change in response to varying conditions.

One of the swallows now looping and whirling about her snatches at a feather, misses, twists round on itself, streaks back, snaps its beak shut on it, and flings itself across the field. Another swallow seizes a feather and flies up, but, flapping and turning loses it to a third swallow, who soars with it even higher and disappears.

-Vermont state poet Galway Kinnell (2006)

Introduction

Tree Swallows (*Tachycineta bicolor*) are cavity-adopters, and frequently nest in artificial nest boxes. In artificial nesting colonies, intraspecific competition for nesting sites and other resources can be intense (Kuerzi 1941). Tree Swallows use feathers to line their nests, and contests for these feathers are easily observable. Competitions over feathers often last for a minute or more and usually involve many birds dropping the feather and chasing after one another. There are numerous references to the "feather fighting" behavior of Tree Swallows in the scientific literature (Cohen 1985, Kuerzi 1941, Lombardo 1995, Weydemeyer 1934, Sheppard 1977). However, while many authors mention this phenomenon in passing, few have published on the adaptive significance of this behavior. Here I present my results from a one-season experimental study of Tree Swallow feather contests in Ithaca, NY.

In early April, when Tree Swallow males have secured a territory and have paired with a mate, females begin construction of a cup nest composed of twigs and dry grasses (Kuerzi 1941). Once the foundation of this nest has been constructed, feathers are woven into the cup and are added to line the interior (Kuerzi 1941, Sheppard 1977). These feathers are scavenged from the surrounding area (Low 1933), and a single nest may contain many types of feathers from various species (Austin and Low 1932, Cohen 1985). However, large, light colored, feathers (often from chickens, wild turkeys, or

nesting geese) with considerable plumulaceous (downy) sections at their bases seem to be most commonly used (Forbush 1929, Sheppard 1977).

The use of feathers as nest lining material has important fitness consequences for breeding birds. The insulative properties of feathers are well known (Wainwright et. al 1976), and help maintain nest homeostasis when the female is between brooding/incubation bouts (Winkler and Turner unpub.data). A well-feathered nest may thus permit the female to spend more time foraging (White and Kinney 1974). Feather lining may also offer protection from moisture, abrasion from nest material, and from ectoparasite attack (Cohen 1988, Sheppard 1977, Winkler 1993). Winkler (1993) demonstrated that chicks in well-feathered nests tend to have higher growth rates and lower ectoparasite loads than chicks in poorly feathered nests. Lombardo (1995) and Chaplin et. al (2002) confirmed that chicks in well feathered nests have higher growth rates, although they failed to demonstrate a significant correlation between feathers and ectoparasite loads. Lombardo (1994) did not find a correlation between nest-feathering and the production of fledglings, although he subsequently showed that well feathered nests had shorter incubation times and fledged significantly more offspring (Lombardo et al. 1995). Sheppard (1977) also showed a direct relationship between numbers of feathers in the nest and the production of fledglings.

Traditionally, aerial competition for feathers has been explained through citing the importance of feathers as nest-lining material (Cohen 1985, Kuerzi 1941, Lombardo et al. 1995, Sheppard 1977) and assuming that feather contests were unavoidable intraspecific battles over a precious breeding resource. However, very frequently a bird that has just acquired a feather will fly *towards* other birds in the colony, and will often

drop and catch the feather close to conspecifics instead of flying directly back to the nest to deposit the feather as one might expect. Furthermore, birds are often observed flying into their nest box with a new feather only to quickly leave their nest again, drop and catch the feather several times, then return to the box and deposit the feather. It thus often appears that feather carriers have the ability to deposit the feather into the box whenever they desire, but sometimes choose not to do so. Such behaviors indicate that an aerial feather contest is more than a simple, all-out competition over an important resource. The goal of this study was to explore the natural history of feather competition behavior and to examine the proximate and ultimate influences on feather contest behavior. This was accomplished through experimental manipulation of nest feathering in the nests of feather-gathering birds and of the feathers presented to them, together with subsequent observation of individual and aggregate behaviors during feather contests.

Methods

The colony I studied is an array of 40 nest boxes arranged linearly 10 meters apart on either side of Mineah Road, a gated, little-used dirt road just outside of Ithaca, NY. This colony is surrounded by agricultural fields, interspersed with tree stands and small residential developments. Feather contests are best incited early in the morning by aerial release of feathers (Forbush 1929). In this study, I launched feathers from a PVC "blowgun" 2.4 m long and 2 cm in diameter to which was taped a 0.2 m piece of 5 mm plastic tubing at one end. A feather was placed, base (plumulaceous) side in, into the lumen of the narrow tubing at the end of the blowgun, which was then held vertically and the feather released into the air with a puff of air from the opposite end of the blowgun.

Feathers were launched between 0530 and 0900 hrs on mornings between 23 May and 27 June, weather permitting.

To involve as many birds as possible, feathers were launched at multiple sites along the road, although not every launch resulted in a feather contest. Most contests began with launches from the center of the colony where bird density was highest. As in other studies, I found that most successful launches occurred on dry, breezy mornings that facilitated feather floating (Cohen 1985). Not all birds near the point of launch joined a feather contest [1], and frequently, Tree Swallows from more than 50 meters away would join the competition[2]. Participation was highly variable from day to day, among individuals, and among near-to-launch and far-from-launch participants. This variability, combined with a random assortment of release points along the road effectively minimizes any bias on contest composition or behavior resulting from the locations of feather launches.

White chicken contour feathers obtained from a local game farm were used for this experiment[3]. Feathers averaged 7.0 cm long and 2.5 cm wide. These feathers appeared (visually) to have little or no ectoparasite load. Feathers were uniquely numbered with Sharpie® permanent marking pens and recovered from boxes at the end of the season to confirm contest winners. All feathers contained some plumulaceous barbs near the bottom of the feather. In an effort to test the effect of feather properties on

[1] Some individuals *never* participated in feather competitions, despite repeated launches near their boxes. In some cases, neither individual in a pair *ever* participated, yet their nests were lined with feathers.
[2] In addition to Tree Swallows, on several occasions Barn Swallows (*Hirundo rustica*) appeared over the Tree Swallow colony, immediately took possession of the feather, and disappeared out of sight. Interspecific competition for feathers merits further investigation, though presentations of feathers at a nearby Bank Swallow (*Riparia riparia*) colony resulted in no feather gathering.
[3] Exception: On 6/4/07, due to the large number of contests that day, wild turkey feathers (*Meleagris gallopavo*) were used when I ran out of white feathers. The type of feather used had no effect on any contest behaviors, and previous literature supports this lack of feather specificity (Austin and Low 1932).

feather desirability and contest behavior, I completely clipped approximately 1/3 of the barbs from the base of the rachis, effectively eliminating the downy part of the feather. These clipped feathers, which comprised half the feathers offered, were released randomly with respect to non-clipped feathers. I hypothesized that less-insulative clipped feathers would be less desirable as nest insulation, and as such, may decrease aggressive contest behavior and/or be dropped more. Conversely, if clipped feathers were easier to carry without interfering with the bird's vision (Winkler, pers. comm.), fewer drops may be observed.

Birds were captured with mist nets around the nest-box or in the box by using hole-blocking "wig-wag" traps manually triggered with fishing line. Playback of Tree Swallow calls and custom-made spinning-wing decoys were used to attract birds towards mist nets (see Fig. 3 in Appendix for description of decoys). Birds were measured, banded, and bled (for other studies), and, to allow for mid-air identification, each bird was marked with a unique color pattern on the breast feathers using permanent ink markers. This coloring lasted for up to two weeks, and some birds were recaptured and their markings refreshed.

In a resource-removal experiment, I removed all feathers in the nest-lining at three-day intervals. I hypothesized that if feather insulation is truly an important determinant of nest success, the behavior of feather-removal birds would change as a result of the manipulation. As clutches were completed, I selected one out of every five active nests (on average) as feather-removal nests, and continued this selection process throughout the breeding season out of necessity because of weather-caused nest failure and re-nesting, and also in an attempt to include early- and late-nesting birds in both my

experimental and control groups. Feather-removal nests were chosen randomly with respect to individuals, but, because feather competitions often occur between neighboring individuals (Sheppard 1977), removal nests were chosen in an ordered alternating fashion to promote feather contests between experimental and control birds. Because of an unusually high rate of nest failure and second (and third) attempts throughout upstate New York during the 2006 season, there were effectively three periods in which I removed feathers from three different sets of nests (see Fig. 4 in Appendix for map and dates of experimental and control nests). After incubation began, I extracted all feathers from feather-removal nests at 3-day intervals. Following Winkler (1993), control nest boxes and their contents were disturbed to a similar extent on a similar time scale, but no feathers were removed.

Birds were observed through binoculars during feather competitions, and contest parameters were narrated into a voice recorder and were later transcribed. Making observations on each individual during a contest was extremely difficult, and although videotaping was attempted, it proved to be ineffective. Therefore, the data for any given contest may be at least partially incomplete. However, observations of multiple contests allowed me to aggregate contest parameters on the behavior of individuals across many contests.

Table 1

Aggregate Contest Parameters

Date	Number of **pursuer** contacts
Time of day	Number of feather **carrier** drops
Contest duration	Number of feather carrier trips to the nest
Number of birds	Sex of feather winner
Number of feather-removal birds (either sex)	Nesting stage of feather winner
Number of males	Seasonal total feathers in winning nest
Number of females	Current attempt number of winning nest
Number of **pursuer** dives	

Table 2

Individual Participant Parameters	
Bandnumber	Age of offspring at contest date
Color code	Attempt number at contest date
Box number	Sex
Experimental?	Age
Contest # participated	Head-bill measurement
Date	Flatwing length
Time of day	Mass
Participation duration	Bred at this colony seasons past?
Number of dives as **pursuer**	Laydate
Number of contacts as **pursuer**	First clutch size
Number of drops as **carrier**	Incubation time
Contest winner?	Nest success: fledge *any* or fail
Nesting stage at contest date	Total fledged
Total dives/total duration of participation from all contests	
Total contacts/total duration of participation from all contests	
Total drops/total duration of participation from all contests	

Over the course of 35 days, data were taken on 317 feather competitions, and individual behaviors were observed for 46 different birds (17 feather-removal, 29 control). A total of 588 feathers were removed from 13 different nests. To go beyond qualitatively characterizing feather gathering, data analysis was performed to answer several broad questions about feathers and feather contest behavior. What factors influence fight behavior? What factors influence contest success, and when are they important? To what extent does nest-feathering affect reproductive success? All statistics were run using SYSTAT 11 (SYSTAT Software, Inc. 2004).

Results

From initial observations, there appeared to be two distinct feather-obtaining behaviors: feather collecting and feather contests. Feather collecting was operationally defined as consisting of short-duration flights of less than 20 seconds involving only one bird. During a feather-collecting event, the feather was returned to the nest box directly,

there were no dives or contacts (because there were no pursuers), and there were no feather drops. Males and females both collected feathers, and this behavior occurred early in the nesting cycle. 42% (n=17) of collecting birds were either constructing a nest or laying eggs, and an additional 38% (n=16) of collecting birds were in the early (<9 days after clutch completion) stages of incubation. The other 20% (n=8) of collecting behavior took place during late incubation or chick-rearing. Collecting behavior was observed in both control and feather-removal birds. Nests where one or both birds displayed the "collector" behavior acquired significantly more feathers than other control birds ($p<0.001$) and averaged more than 80 feathers by the end of the season, while the average control nest contained only 38 feathers. Feather removal nests contained zero feathers at the end of the season. These numbers fall within the range published by Winkler (1993) and Sheppard (1977). Interestingly, I noted on several occasions that a collector's mate (usually the male) guarded the area where I was releasing feathers, chasing away trespassing birds seemingly to ensure that his/her mate had a chance to collect the feather unmolested.

Table 3

Methods of Feather Gathering		
	Feather Collecting	Feather Contests
Number of birds	1	> 1
Duration	< 20 sec.	> 20 sec.
Number of dives, contacts, and drops	0	At least one behavioral variable > 0
Stage of breeding cycle	Nesting, early incubation	Throughout the season

Table 3. Two methods of gathering feathers, and their distinguishing characteristics

Birds that displayed the collecting behavior also took part in feather contests. These birds always dominated contests against other birds: individuals that displayed collecting behavior on more than three occasions also won (deposited the feather in their nest) 100% of competitions with other birds. Collectors, when contestants, dropped the feather less than did non-collectors during feather contests, although this correlation was not significant ($p=0.213$). Collecting behavior was not significantly correlated with feather removal, sex, age, morphology, or other individual parameters; this behavior seems specific to a handful of individuals. Feather collectors fledged fewer chicks than did pure feather competitors ($p=0.03$).

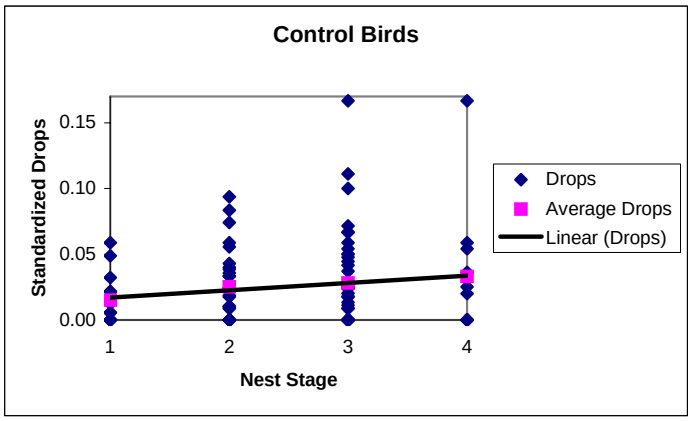
Unlike feather collections, feather contests occurred throughout the breeding cycle and lasted much longer—63 seconds on average, although I observed competitions with durations of up to eight minutes. An average contest consisted of 2.9 birds: 0.75 feather-removal birds (of either sex) 1.03 males, 1.03 females, and the remainder unidentifiable. Newly fledged birds did not participate in late-season feather contests, despite my attempts to involve them. There were an average of 1.02 dives, 1.30 drops, and 1.04 contacts per contest. Averaging across all contests, it took 1.66 trips to a nest box before the feather was deposited. 74% of marked feathers were recovered in the boxes of contest winners at the end of the season. Because there were many re-nests (birds building on top of existing nests and accompanying feathers), I was careful to associate the total number of feathers in the nest with a particular nesting attempt. In some cases, I found two or three nests stacked on top of one another, and thus recorded three feather totals, one for each attempt. The difficulty in finding feathers in matted-down, decomposing Tree Swallow nests at the end of the season almost certainly

accounts for the 26% of feathers that were not recovered. I never observed Tree Swallows intentionally or accidentally removing feathers from the box late in the season, as other research has suggested (Mertens 1977, Møller 1987). Almost all feather recoveries confirmed earlier observations of contest winners, which suggests that once a feather is deposited in the box, it is not removed and fought over again. It also appears that Tree Swallows do not steal feathers from neighboring nests, as has been observed in other swallow species (*Riparia riparia*—Hoogland and Sherman 1976).

Feather properties affect contest behavior. Longer feathers incited more total dives ($p=0.02$), as well as more total contacts ($p=0.014$) and contacts corrected for contest duration ($p=0.006$). Experimentally clipped feathers predicted fewer total contacts ($p=0.01$) and fewer standardized contacts ($p=0.035$). There was a trend towards fewer dives in competitions for clipped feathers, although this difference was not significant ($p=0.111$). There was no effect of feather length, width, or clipping on the number of drops in a contest.

Interestingly, there was a trend toward *more* feather drops in control birds as the season progressed, although this result was not significant ($p=0.098$). In feather-removal birds, there was a highly significant trend towards *fewer* drops per second later in the breeding cycle ($p<0.001$). There were no significant changes in dives or contacts between feather-removal and control groups over the course of the season.

Fig. 1



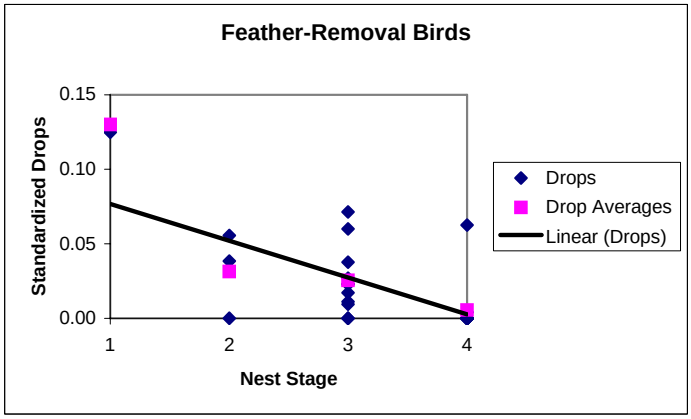


Fig. 1.
Drops/Duration vs. Nest Stage
Nest Stage 1=construction, 2=laying, 3=incubation, 4=feeding

*Note: Only one feather-removal bird was observed dropping the feather during the nest construction stage. This small sample size is due to the fact that I did not begin experimental feather removal until after clutch completion. This feather-removal bird was re-nesting when this data was taken. When this point is removed, the trend remains significant (p=0.021).

Birds successful at winning feather contests made significantly fewer dives/s ($p<0.001$) and fewer contacts/s ($p<0.001$). Interestingly, contest winners also dropped the feather more than contest losers ($p=0.028$). These statistics may be biased in that only feather carriers can perform drops, and only pursuing birds perform dives and contacts. If the initial feather carrier is the eventual contest winner, then my results would be misleading,

as they are not corrected for individual time of feather possession and time spent pursuing. Because of the way in which I collected data, I could not directly correct for this potential bias. However, from the original field narrations, I was able to reexamine 21 competitions containing at least one drop and one dive or contact. Of the 21 initial feather carriers in these contests, only 5 (24%) of these birds eventually won the competition, while 16 (76%) of initial feather carriers lost the contest. This sample indicates that initial carriers do not win more than might be expected by chance, suggesting that the behavior of contest winners can be examined without correcting for which bird carried the feather initially.

Attempts to directly test the effect of individual participant quality[4] on contest success yielded ambiguous results. Birds with larger head-to-bill-tip measurements (higher quality birds) were more often contest winners ($p=0.033$). However, shorter wings and later laydates (lower quality birds) were also significant predictors of contest success ($p<0.001$), ($p<0.001$). Examination of clutch sizes and fledging success revealed nonsignificant trends ($p=0.525$), ($p=0.168$).

It has been proposed that birds may use more feathers earlier in the season when the ambient temperature is colder (White and Kinney 1974). However, I found a significant direct relationship between the number of feathers and first laydate; having more feathers in the nest was correlated with a *later* first laydate ($p<0.001$). However, because of high abandonment rates during laying, it is difficult to be certain that my recorded laydates were not preceded by an earlier abandoned attempt in which the female was not captured. Also, the number of feathers in the nest was strongly correlated with

[4] For the purposes of this experiment, "quality" refers to the physical condition and behavioral strategies of individuals that may affect their ability to hold territories, secure resources, reproduce successfully, etc.

the total number of chicks fledged (p=0.003), even when feather-removal birds were eliminated from the analysis (p=0.019). Because I counted the total number of feathers in the nest per attempt, I can be certain that nests with more feathers were not simply those nests that lasted throughout the entire season. Birds with more average drops per contest and fewer contacts fledged significantly more offspring (p=0.003, p<0.001). Recall that these same trends also described birds classified as contest winners. Feather-removal birds showed a (non-significant) trend towards a longer incubation time (p=0.130), although there was no effect of feather removal on the number of chicks fledged.

The composition of competitors seemed to have little effect on aggregate behavior in that contest. However, a higher ratio of females in the contest was correlated with fewer total contacts/s (p=0.024) and more drops per duration (p=0.044).

Discussion

The existence of two distinct behaviors, as well as high variation and seasonal changes in participation and contest success indicate that feather gathering in Tree Swallows is a more complex behavior than has been previously recognized. In contrast to existing literature, which suggests that males do the majority of feather gathering (Cohen 1985, Kuerzi 1941, Lombardo 1994, Sheppard 1977, Winkler 1993), I found that both males and females participate in feather gathering (collecting and/or competition) with approximately equal frequency. This is noteworthy, because it calls into question theories of feather contests as indicators of male parental investment (Lombardo 1995)and female choice based on male contest performance. While aerial feather competition may have some merit as an indicator of individual quality (see later

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discussion), it seems unlikely that this behavior can be used to measure potential for other male parental investment. I also found that contests continue throughout the breeding cycle, although participation is highest during incubation and there is a decline in participation during chick feeding. This suggests that feathers are important throughout the nesting season, not only in the cool, early spring weather. Although the proximate benefits of feather insulation were not examined in this study, my results support the notion that feathers offer protection from not only cold[5], but also abrasion, moisture, and/or parasites that may affect the offspring throughout the entire breeding season (Cohen 1988, Sheppard 1977, White and Kinney 1974).

Collecting behavior was specific to a few individuals in my study population, although this behavior could not be predicted by age, sex, or morphology. This intense feather gathering behavior persisted throughout the breeding season, and these birds continued to express the collector "personality," (intense, purposeful feather gathering) even when participating in feather contests. Interestingly, the high-efficiency collector "personality" did not develop in competitors with feathers removed from their nests. This may indicate that collecting behavior has a strong genetic component, and may be a competing evolutionary strategy to feather competition, with different costs and benefits.

Collectors frequently won feather contests, dropped the feather less, and on average had more feathers in the nest than birds only participating as feather contestants. However, despite having well-feathered nests, collectors fledged fewer chicks than competitors, and, because the number of feathers in the nest is generally correlated with fledging more offspring, it follows that feather lining is not the most important factor in

[5] In accordance with published results (Lombardo et al. 1995), feather-removal birds had (nonsignificantly) longer incubation times.

fledging chicks. If the total number of feathers in the nest were the most important determinant of reproductive success, collectors would have a higher reproductive output on account of higher feather totals. Thus, it seems that collectors, while skillful at gathering feathers, may be of lower-quality in some other, more important way (inferior genes, poor parents, etc.). It would be interesting to examine why collecting is specific to only a few individuals, and why these individuals fail to fledge as many chicks as non-collectors. It is also important to study the repeatability of this behavior between seasons and within families, which would reveal whether collecting behavior is peculiar to the environment in a given breeding season, and whether this behavior has a strong genetic basis.

The influence of feather properties on contest behavior can be explained by viewing the feather contest from a pursuing bird's perspective. Longer feathers protrude farther from the carrier's bill than shorter feathers. Thus, longer feathers are probably much more visible to pursuing birds. A carrier of a long feather is an easily identifiable target, and falls victim to many more pursuer dives and contacts than a carrier who possesses a short feather. Other published accounts note that contests are best incited by large, white feathers, and an increased visibility hypothesis explains these results (Cohen 1985, Sheppard 1977).

This visibility explanation also accounts for the behaviors observed in competitions for experimentally clipped feathers. Feathers were measured before they were clipped; however, trimming these feathers made them of comparable visibility to shorter unclipped feathers. Therefore, it is not surprising that I observed fewer dives and contacts over these less-visible clipped feathers. Originally, I had hoped to alter the

desirability of feathers by clipping the insulative down from the rachis. I hypothesized that clipping the down might result in more feather drops if clipped (less insulative) feathers were less desirable. Conversely, fewer drops may be observed if clipping the down increases the ease of carrying the feather. Because drop frequency is the best measure of desirability (assuming drops are mostly voluntary), and no change was observed in drop frequency with feather clipping, I conclude that my experimental manipulation did little more than create a second class of short feathers. If the "fluffiness" (extent of the downy part) of the feather had an effect on the desirability of that feather, I would have observed a difference in voluntary drops between short (and "fluffy") feathers and (short, but not "fluffy") clipped feathers.

Among birds participating in feather contests, my results may be explained by placing individuals into one of two groups: birds that have feathers in the nest at the time of the contest, and birds that do not. The number of feathers in the nest is determined in part by contest success; if feathers are not removed from the nest, birds successful in bringing feathers to the nest will accumulate them as the season progresses. Behavioral differences between the feather "haves" and "have-nots" are best understood from the perspective of the individual, and reflect an individual's desire to line the nest with at least a threshold number of feathers. After this threshold point, adding additional feathers has diminishing returns or may even be costly in some situations (Lombardo 1994, Møller 1987).[6] Based on end-of-the-season observations, 30-40 feathers is a good estimate of this threshold number for the population I observed. Birds on a given contest

[6] This point may not be a pure number; it is important to experimentally determine if such a threshold is universal, or to what extent it varies with conditions and between individuals. It is likely that the number of feathers used in the nest is subject to natural selection (balance between feather benefit and gathering cost).

date may have more or fewer than this number of feathers, and my results suggest that this affects their behavior.

Because feather competition occurred throughout the breeding cycle, my data tracked contest behavior as threshold feather numbers are approached in each nest. The behavioral results of this progression can be observed by examining seasonal variability in drops between control and feather-removal birds, which indicates a changing desire to add more feathers to the nest. Control birds, as they acquire more and more feathers throughout the season, reach and may surpass the threshold number of feathers in the nest. Thus, later in the season with the threshold already attained, feather gathering becomes less important to control birds, and a larger number of drops is observed. Conversely, in feather-removal birds, the number of feathers in the nest is consistently below the threshold value. Feathers are important during late incubation and chick-rearing; therefore, as the breeding cycle progresses, feather-removal birds become more focused on feather gathering, and they drop feathers less frequently. It is interesting that these removal birds do not “flip” into high-efficiency feather-collecting behavior. The fact that they do not reinforces my impression that aerial feather competition and feather collecting are distinct behaviors, and are not easily interchangeable.

Birds with feathers removed from their nests may win more contests later in the season: among contest winners in the chick-rearing stage (n=28), 54% were feather-removal birds. In contrast, of contest winners in the incubation stage (n=95), only 17% of individuals were feather-removal birds. While these numbers are clearly biased by differential participation between removal and control birds, it is still be possible to draw conclusions. There are two explanations for control bird behavior during chick-rearing:

either control birds are participating less, or are participating the same amount and are winning less. In either case, the implication is that feather-removal birds late in the breeding cycle are working harder than control birds to obtain feathers.

Birds that are successful at winning contests make fewer dives and contacts and, in general, tend to drop feathers more frequently. This implies that contest winners are not necessarily the most aggressive competitors, or that aggressiveness is variably effective across a breeding season. Early in the season, the number of feathers in the nest is low for all birds. Early season fight winners may be better-quality birds (I will refer to this as the "individual quality hypothesis") that are able to obtain the feather cleanly in the midst of a fight (Sheppard 1977), without many dives or contacts. These birds may then drop and catch with impunity before taking the feather back to the box (Gibbs 1981). Possible explanations for these early season dominance displays are explored later. As the breeding season progresses and early-season contest winners meet the threshold number of feathers, these birds drop more, but are not as frequently contest winners. These late-season results (many drops, few wins) are overshadowed by the large amount of early-season data (many drops, many wins), and reduced participation by early-season winners.

Attempts to find direct correlations between morphology and individual quality yielded ambiguous results. This was not unexpected, as previous research by Winkler and Allen (1996) also found no correlation between morphological measurements and individual quality. Winkler and Allen (1996) demonstrated that laydate is a good predictor of quality in Tree Swallows; following this, my results indicate that later-laying (lower-quality) birds win significantly more contests than high-quality birds. This result

conflicts with the hypothesis that higher-quality birds are winning early season fights. However, I am suspicious of a later laydate predicting contest success, because of the unique early-season conditions in 2006. Early-season cold snaps likely prevented some high quality birds from nesting until later in the season. In addition, many early-season clutches were abandoned before completion, and there are thus no records for the female on that nest. If she re-nested and was subsequently captured, I would have an incorrect value for her first laydate (as well as her first clutch size). While laydate is usually a good measure of individual quality in nesting Tree Swallows, the unique breeding conditions in 2006 lead me to doubt the validity of this metric.

The individual quality hypothesis is supported by behavioral/reproductive output similarities; the same behaviors that characterized early season contest winners (few dives and contacts, many drops) were correlated with a greater number of chicks fledged. The individual quality hypothesis is also supported by a previous study by Sheppard (1977). If this hypothesis is correct, it implies that high-quality birds frequently won feather contests early in the season, quickly filled their nests with at least the threshold number of feathers, and fledged a large number of offspring.

It logically follows from this hypothesis that low-quality control birds frequently lost early season feather contests. The individual quality hypothesis implies that when a low-quality bird dropped a feather early in the season, it was frequently picked off by a higher-quality bird, forcing the former carrier to aggressively chase the high-quality bird without success. As a result, these low-quality birds would have fewer feathers in their nest. Because they have poorly-insulated nests and are generally of low quality, these birds tend to fledge fewer offspring. Although these predictions made by the individual

quality hypothesis are consistent with the current data, further research is needed to test this hypothesis thoroughly.

Feather-removal birds likely contained both high- and low-quality individuals. If genetics and good parenting are more important to offspring production than how many feathers are lining the nest, this would explain why the feather-removal experiment had no effect on the number of offspring fledged. Likewise, if the experimental group contains both high- and low-quality individuals, feather-removal would have no effect on the chances of winning early season fights, and indeed this was observed. Experimental removal was correlated with fewer drops later in the season, and may be related to competition success, implying that these birds were working hard to fill their nest with the threshold number of feathers.

Fig. 2

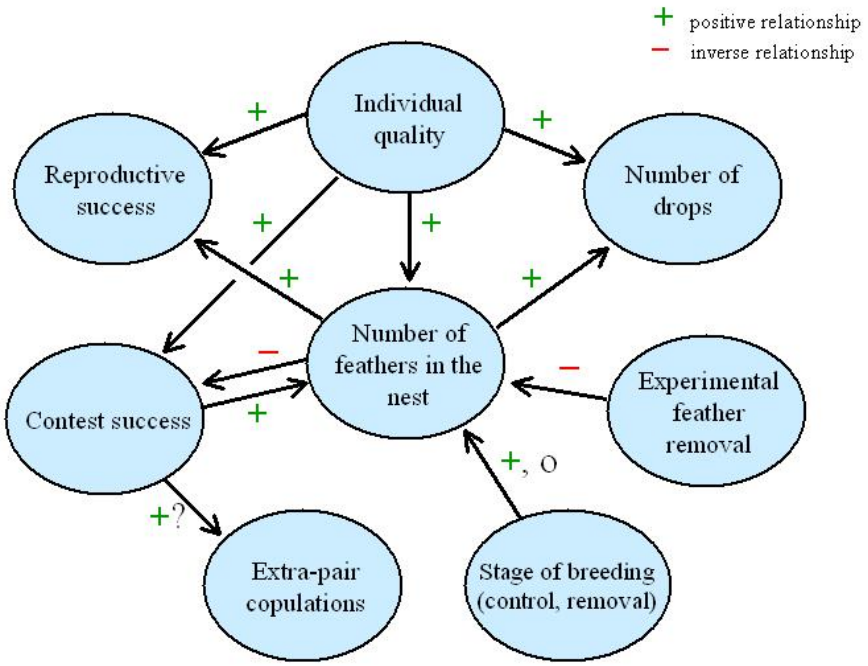

Fig. 2. Provisional path diagram suggesting causes and effects of aspects of contest behavior, and how they interact

The 2006 breeding season in Ithaca, NY, was interrupted by two separate cold snaps that often resulted in the death or abandonment of at least one individual in a breeding pair. Some birds made as many as three attempts before finally succeeding in raising chicks. More feathers in the nest (per attempt) was correlated with a later laydate, perhaps reflecting the time budget of individuals faced with harsh conditions early in the breeding season (White and Kinney 1974). Logically, if earlier laying birds are preoccupied with finding food in tough conditions, then feather gathering may be superceded by basic survival needs. This result may be unique to the unusually unforgiving weather during the 2006 season, but it does contradict the notion that earlier laying birds facing cool conditions will gather more nest insulation. In fact, one might expect that earlier-laying nests would have *more* feathers than usual because of the harsh conditions in 2006. Other studies have found no relationship between nest feathering and laydate (Lombardo 1994). Experimental manipulations are needed to disentangle the interaction between laydate and the number of feathers in the nest. Having more feathers in the nest was strongly correlated with fledging more offspring, even when experimental birds were excluded from the analysis. This supports the results of previous studies that have shown feathers to be important for reproductive success (Lombardo et al. 1995, Winkler 1993).

This study necessarily had a broad focus, as it was the first examination of this behavior. The results of this study are numerous and diffuse, and it is difficult to assemble these into a complete picture, given the time constraints of this project. My goal was to develop experimental protocols and a framework to guide future research. Each of my results deserves to be examined separately. Once the results of several

narrowly focused projects have been synthesized, we may be able to better grasp the true nature of this behavior. Here I highlight five important results of this study, some of which are very well-supported by my data, and some of which may serve as a springboard for future research. 1) There exist two distinct feather gathering personalities (feather collecting and feather competing), and these behaviors are specific to individuals. 2) Feather properties can affect contest behavior; longer feathers are competed over more aggressively, possibly because they are easier for pursuing birds to see. 3) The number of feathers in the nest appears to be a determinant of contest behavior, especially late in the season. 4) Early season contest behavior is determined by other factors; individual quality remains a leading hypothesis. 5) The number of feathers in the nest plays a significant role in reproductive success, but there are certainly other important factors that must be taken into account.

Conclusions

My results are in accordance with a theory of individual quality being a determinant of contest behavior, contest success, the number of feathers in the nest, and the number of offspring fledged. Many of these variables feed back on one another, and some associations are stronger than others. At least one question still remains: why do Tree Swallows intentionally drop feathers? It seems more logical to not partake in feather contests once a nest is well-feathered; however, I still observed participation (albeit reduced) late in the season. Also, feather dropping seems to be clearly linked to the number of feathers in the nest at the time of the contest (and a decreased desire to add more), but this cannot account for the occurrence of early-season drops.

It is possible that feather competition has implications for extra-pair reproduction. If it is difficult to drop and catch the feather without losing it to another bird, then this may be in itself an honest indicator of individual quality. One interpretation of my results suggests that high quality birds are in fact dropping and catching the feather amongst inferior conspecifics. Given the highly visible nature of feather contests, it seems reasonable that these competitions may be a good opportunity for high-quality birds to "show off," in hopes of garnering extra-pair copulations (EPCs). These displays are common earlier in the season, when the chances of obtaining EPCs are good. Perhaps this is why a higher female ratio was correlated with fewer contacts and more drops; males might be more likely to display when there are females present. Clearly, there is the potential for EPC benefits that accompany showy feather fighting, and parentage studies would be needed to test this theory. I am currently developing protocols to examine this in the 2007 breeding season.

Future work must examine individual participants more closely, tracking the daily number of feathers in the nest, and examining many measures of participant quality. Also, feather contests need to be further broken down, noting the initial feather carrier, and recording both drop-catches by the same bird as well as changes of possession.

There are many competing theories that remain to be examined. For example, it is possible that feather competitions help birds hone their aerial insectivore skills that will be required after hatching (Mandel, pers. comm.), and studies of comparative feeding rates between high-quality and low-quality competitors could yield interesting results. EPC studies are needed to help establish whether feather contests may convey reproductive benefits to good feather competitors. Longitudinal studies might examine

whether individual behavior is consistent across seasons, or whether feather-gathering behavior is a plastic response to variable conditions.

Finally, it is possible that feather competition in Tree Swallows is an example of animal play behavior. The three main types of animal play, locomotor play, object play, and social play, have all been observed in various species of birds (Fagen 1981 and references therein). Specifically, drop-catch play is common in birds of prey, gulls, and corvids. Social chasing play has been documented in harriers and parrots, among others (Burghardt 2005 and references therein). Feather competitions have not been formally studied as a potential play behavior, although they possess many defining characteristics of play, and would seem to lie at the nexus of object and social play. See table 4 in the Appendix for a short treatment of how feather contests may be categorized as animal play.

A well-feathered nest conveys reproductive benefits, and the ways in which individuals obtain this resource are clearly important. However, aerial feather competitions in Tree Swallows have received little attention in previous studies. This fascinating behavior is closely tied to within-pair reproductive output, and may also play a role in extra-pair matings. More research on this behavior is sorely needed; the adaptive significance of this complex phenomenon will only be revealed through careful experimentation and observation.

Acknowledgements

Most importantly, I would like to thank David Winkler, my research advisor, for his invaluable help and guidance throughout this project. This study was funded by the Howard Hughes Summer Scholars program, and I would like to thank Laurel Southard and Pamela Davis for their help during the program. I am grateful to the Winkler lab for their ingenuity and constructive criticism, and for much needed help with statistics. Finally, thanks to Abraham Katzen, Sharri Zamore, and Emily Parrott for helping with trapping and banding, and for tolerating my enthusiasm for feather fights.

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Appendix

Fig. 3

I created spinning-wing Tree Swallow decoys, following the successful model used by some duck hunters in the United States. I used aluminum foil, modeling clay, and paint to craft the shape of a swallow fluttering at the hole of a nest box, then drilled a hole transversely through the body at the level of the wings. I used a plastic drinking straw and colored tagboard to create the wing shapes and I mounted the decoy on small dowels, to the bottom of which I attached a small motor (used in childrens' toys). I used a rubber band and more clay to create a crude belt and pulley system running from the drive shaft of the motor to the drinking straw axel. I attached this assembly to a board with a switch and battery mounted below. This board could then be attached to the nest box in such as way as to make the "flapping" swallow appear to be about to enter the box. This decoy, when combined with playback and mist nets surrounding the box, was highly effective at luring and capturing territorial males before clutch initiation.

Fig. 4

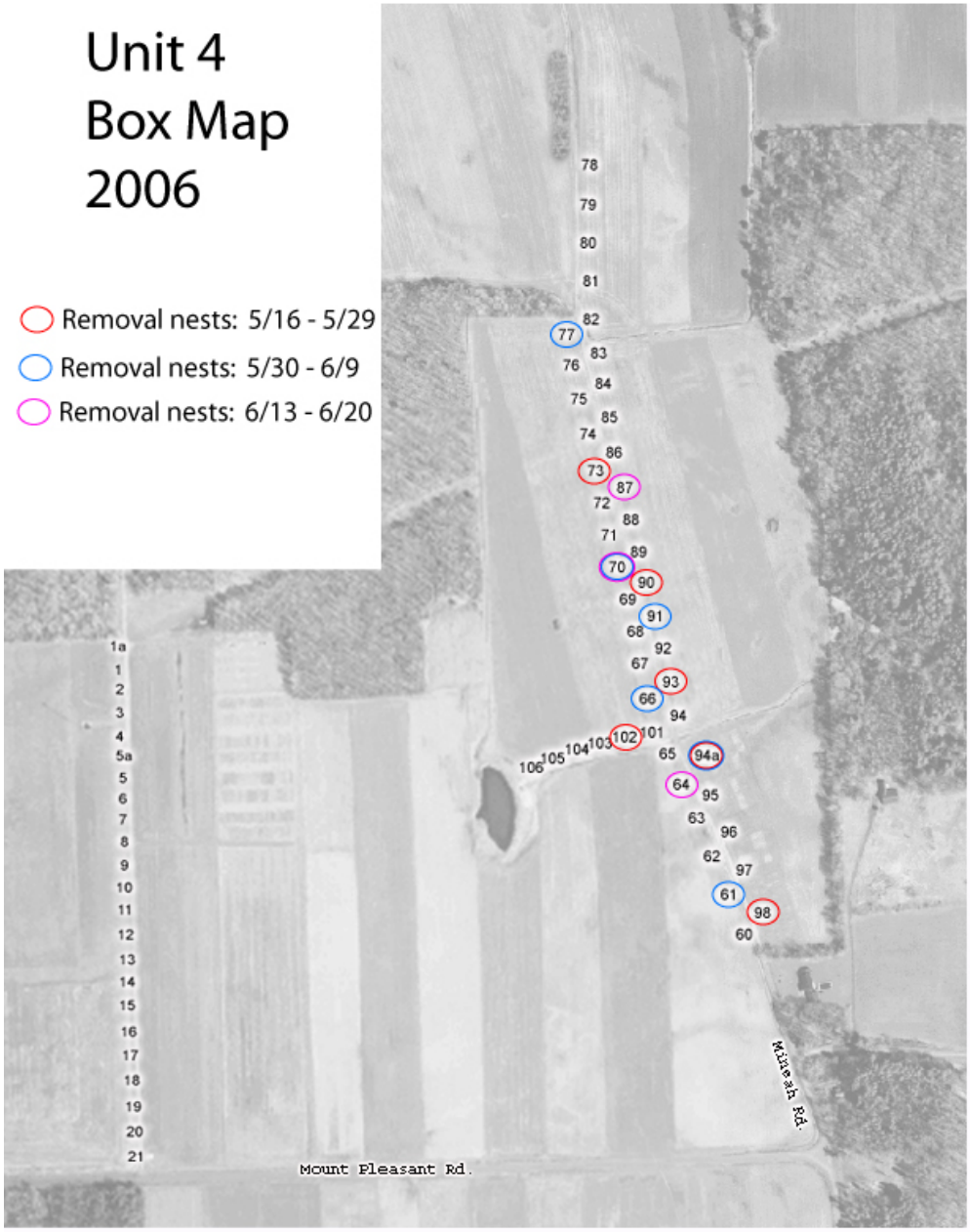

Fig. 4. Nests from which feathers were removed, categorized by date of removal

Table 4

Feather competition characteristics that support the play hypothesis are shown in green, and those that conflict are shown in red. When relevant, the more common behavior is listed first.

Defining characteristics of play

General characteristic	Feather contest correlate
No immediate function	Dropping a feather Gathering feathers for nest lining
Object being played with is valueless	Many initial feather carriers lose the fight, and drops are likely intentional Feathers are an important resource
Quick and energetic motions	Chasing, diving
Motions are repeated, but are sequentially variable	Diving, dropping, contacting
Exaggerated, incomplete, awkward	Exaggerated loops
Common in juveniles	Juvenile swallows were presented with feathers, but none participated
Existence of "play" signals	Dropping a feather, vocalizations
Mixing of behavior from several contexts	Diving from territory defense, feather catching from aerial insect capture
Absence of external stressors	Feather contests occur in my presence Feather contests less common in cold weather (Ringelman, pers. obs.)
Absence of consummatory acts	Feathers are usually taken into the box Feather is sometimes dropped to the ground

*This table of general play characteristics is adopted from Burghardt (2005), with some parameters from Fagen (1981).