RESEARCH ARTICLE

Feather-chewing lice and Tree Swallow biology

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ABSTRACT

Feather-chewing lice (Order Phthiraptera, Suborder Ischnocera) commonly infest birds and may affect their survival and reproduction. From 1993 to 2005, we examined several aspects of the biology of breeding Tree Swallows (*Tachycineta bicolor*) potentially associated with holes in wing and tail feathers caused by feather-chewing lice. Most individuals had <10 feather holes, but 90% of second-year (SY) females, 68% of after-second-year (ASY) females, and 80% of males had ≥1 feather hole. ASY females had significantly fewer feather holes than SY females and males. There was evidence of positive assortative mating for feather hole number between ASY females and their mates. SY females and their mates did not differ significantly in the number of feather holes, but ASY females had significantly fewer holes than their mates. Males with fewer feather holes were heavier and had longer right wings. Feather hole abundance was not significantly associated with reproductive performance. Feather hole abundance was not associated with whether females bred 1 time or >1 time at our study site, but males with fewer holes were more likely to breed >1 time. Mean feather hole abundance differed significantly among years for SY females and males that bred 3 and 4 times, respectively, but not for ASY females that bred 4 times. Collectively, these data suggest that feather-chewing lice, as estimated by the damage they cause to wing and tail flight feathers, have little effect on Tree Swallow fitness.

Keywords: feather-chewing lice, feather holes, Ischnocera, *Tachycineta bicolor*, Tree Swallow

Piojos masticadores de plumas y biología de *Tachycineta bicolor*

RESUMEN

Los piojos masticadores de plumas (Orden Phthiraptera, Suborden Ischnocera) comúnmente infestan a las aves y pueden afectar su supervivencia y reproducción. De 1993 a 2005, examinamos varios aspectos potencialmente asociados de la biología de los individuos reproductivos de *Tachycineta bicolor* con agujeros en las plumas del ala y la cola causados por piojos masticadores de plumas. La mayoría de las golondrinas presentaron menos de 10 agujeros en las plumas pero 90% de las hembras del segundo año, 68% de las hembras de más de dos años y 80% de los machos presentaron al menos un agujero en las plumas. Las hembras de más de dos años presentaron significativamente menos agujaron en las plumas que las hembras de dos años y los machos. Se encontró evidencia de un apareamiento selectivo positivo de acuerdo al número de agujeros en las plumas entre las hembras de más de dos años y sus parejas. Las hembras del segundo año y sus parejas no difirieron significativamente en el número de agujeros en las plumas, pero las hembras de más de dos años presentaron significativamente menos agujeros que sus parejas. Los machos con menos agujeros en las plumas fueron más pesados y presentaron alas derechas más largas. La abundancia de agujeros en las plumas no estuvo significativamente asociada con el desempeño reproductivo. La abundancia de agujeros en las plumas no estuvo asociada con el hecho de que las hembras hayan tenido crías una vez o más de una vez en nuestra área de estudio, pero los machos con menos agujeros tuvieron mayor probabilidad de criar más de una vez. La abundancia media de agujeros en las plumas difirió significativamente entre años para las hembras del segundo año y los machos que criaron tres y cuatro veces, respectivamente, pero no para las hembras de más de dos años que criaron cuatro veces. En conjunto, estos datos sugieren que los piojos masticadores de plumas, según lo estimado por el daño que causan a las plumas del vuelo del ala y la cola, tienen un efecto menor en la adecuación biológica de *T. bicolor*.

Palabras clave: agujeros en las plumas, Ischnocera, piojos masticadores de plumas, *Tachycineta bicolor*

INTRODUCTION

An enduring problem in modern natural history studies is identifying the causes of selection. Parasites have attracted attention as possible causes of selection because they are ubiquitous and negatively affect the survival and reproductive success of their avian hosts (e.g., Brown and Brown 1996, Clayton and Moore 1997). Field ornithologists have focused most of their attention on the effects of ectoparasites on their hosts, probably because detecting their presence is relatively easy compared with detecting endoparasites (Clayton and Moore 1997, Wilson et al. 2002).

Birds are commonly infested with feather-chewing lice (Order Phthiraptera, Suborder Ischnocera) that feed on the nonliving keratin of feather barbules (Janovy 1997, Johnson and Clayton 2003). Feeding by ischnoceran lice produces pin-prick-sized holes in the primary and secondary feathers of the wings and in tail feathers (Vas et al. 2008). Because feather holes damage feathers, they have the potential to negatively affect fitness in several non–mutually exclusive ways. First, holes in flight feathers break up the continuity of the flight surfaces, thereby allowing air to move through the holes, reducing aerodynamic efficiency (Norberg 1990; although the aerodynamic effects of feather holes need experimental examination). Second, feather holes may increase feather breakage (Kose et al. 1999, Barbosa et al. 2002), negatively affecting the aerodynamic properties of wing and tail feathers. Third, feather holes may result in increased metabolic rates by increasing the amount of time spent in energetically expensive flapping flight (Barbosa et al. 2002). These negative effects suggest that ischnoceran infestations may be important causes of selection in birds (Pap et al. 2005). Finally, feather holes, by exposing the medulla of feathers, may increase their susceptibility to damage from feather-degrading bacteria (Burtt and Ichida 1999).

Our goal was to examine the possible role of feather-chewing lice as a cause of selection in Tree Swallows. We counted feather holes caused by lice, rather than counting lice, because we know that in European Barn Swallows (*Hirundo rustica*), feather hole and louse abundance are strongly positively correlated (Barbosa et al. 2002) and feather hole abundance covaries with feather breakage (Kose et al. 1999), flight performance (Barbosa et al. 2002), immunity levels and arrival dates (Møller et al. 2004), song characteristics (Garamszegi et al. 2005), and mate choice preferences (Kose et al. 1999), which all suggests that feather-chewing lice may also be a cause of selection in Tree Swallows. To evaluate the potential of feather-chewing louse infestations as causes of selection in breeding Tree Swallows, we examined relationships between feather holes and patterns of assortative mating, morphology, reproductive performance, and return rates.

METHODS

Field Methods

We studied the relationships between various aspects of the biology of breeding Tree Swallows and louse-chewed feather holes in individuals that bred during 1993–2005 in wooden nest boxes mounted on metal poles erected in grids in old fields on the campus of Grand Valley State University (GVSU), Ottawa County, Michigan (42°57′N, 85°53′W), USA (Johnson and Lombardo 2000).

Breeding Tree Swallows were categorized for analyses as either (a) second-year (SY) female ($n = 150$), (b) after-hatching-year (AHY) female ($n = 43$), (c) after-second-year (ASY) female ($n = 305$), or (d) male ($n = 432$), based on their sex and plumage characteristics, following Dwight (1900), Hussell (1983), and Winkler et al. (2011). We focused our analyses on SY and ASY females and their mates because of the relatively small proportion of breeding AHY females (9.5% of all females).

We began monitoring breeding activity on about May 1 of each year. Clutches were never initiated before that date. We recorded clutch initiation date, clutch size, and the number of fledglings produced from each nest to evaluate reproductive performance. Data from nests lost to predation were not included in analyses of reproductive performance.

We captured birds at their nests (Yunick 1990) throughout the breeding season and measured their mass, bill length, unflattened right wing-chord length, and depth of the right tail fork (Winkler et al. 2011) and color-marked them to facilitate individual identification. We banded birds with federal bands to identify individuals that bred multiple times or had fledged from nests at GVSU. We captured >95% of breeding Tree Swallows each year.

We counted the numbers of holes in the primary and secondary feathers of both wings and tail feathers and used the sum of these counts in analyses. Our methods require several caveats. First, we did not identify the species of feather lice infesting our study birds. However, the feather holes found in Barn Swallows and several other small passerines are likely caused by lice of the genus *Brueelia* (Vas et al. 2008). *Brueelia* spp. are found mostly on passerines and tend to be very host specific (Johnson et al. 2002). *Brueelia* spp. disperse to new hosts on hippoboscid flies (Johnson et al. 2002, Johnson and Clayton 2003) and during physical contact between hosts (Rékási et al. 1997, Brooke 2010).

Second, we did not quantify feather-chewing lice, so we did not directly test our assumption that feather hole number estimated louse abundance. However, tail feather hole and louse abundance were strongly positively correlated in Barn Swallows (Barbosa et al. 2002), which supports our assumption.

Third, feather hole counts may overestimate the prevalence of ischnoceran lice because feather holes may also be caused by anomalies during feather growth that produce feather abrasions similar to the holes chewed by lice (Bortolotti et al. 2002). Notwithstanding Bortolotti et al.'s (2002) suggestion, we think that our counts of feather holes produced accurate estimates of not only feather damage from activities of feather-chewing lice, but also their abundance (Clayton and Walther 1997).

Statistical Analyses

We examined data for normality and used parametric or nonparametric statistical analyses, where appropriate, in IBM SPSS Statistics version 20.0 for Windows (IBM 2011) and SAS version 9.3 (SAS 2011). M.P.L. made all morphological measurements and counted louse holes to avoid interobserver variation.

We used methods described in Rózsa et al. (2000) and QPweb (Reiczigel et al. 2013) to analyze and report abundance, intensity, and prevalence of feather holes. Feather hole abundance is the number of feather holes found in all birds, including those with no feather holes. We report feather hole abundance as means $\pm$ SE. Feather hole intensity is the number of feather holes in birds with ≥ 1 hole; birds with no feather holes are excluded from this calculation. Feather hole prevalence is the proportion of all birds with feather holes. We report feather hole intensity and prevalence as mean $\pm$ 95% confidence interval.

We used QPweb to calculate the degree of aggregation (k) and index of discrepancy (D) of feather holes. As feather hole aggregation increases, k approaches 0; $k < 1$ is typical of most macroparasitic infections because most hosts have few parasites whereas only a few hosts have many (Wilson et al. 2002). The index of discrepancy quantifies aggregation as the discrepancy between the observed distribution and a hypothetical one in which all hosts are equally infected; D ranges from 0 (i.e. no aggregation) to 1 (i.e. all parasites are located in 1 host) (Poulin 1993). To avoid pseudoreplication, our calculations of k and D used feather hole count data collected the first time we measured a breeding bird. Most of our analyses focused on feather hole abundance because it estimated feather damage likely to have negative effects on flying ability (Norberg 1990) and, thus, survival.

To investigate the relationships between feather hole abundance and the date that feather holes were counted, morphological measures, reproductive performance data, and return rates, we used generalized linear mixed models (GLMMs) (Bolker et al. 2009) in PROC GLIMMIX in SAS. PROC GLIMMIX automatically scales the variance with the overdispersion parameter for GLMMs. The generalized chi-square statistic measures the residual sum of squares in the final model, and the ratio with its degrees of freedom is a measure of variability of the observation about the

mean model. The ratio between the Pearson chi-square and the degrees of freedom provides information on the variability of the model; a ratio close to 1 indicates that the variability has been properly modeled and that there is no residual overdispersion. We report instances of over-dispersion, which occurs when the residual deviance is greater than the residual degrees of freedom and tends to arise when 1 or more factors that were not measured during the study have an important effect on response variables (Crawley 2002, Bolker et al. 2009). It may also occur if an incorrect error distribution is specified—that is, if the probability one is attempting to model is not constant within each cell but behaves like a random variable, resulting in an inflated residual deviance (Crawley 2002).

On the basis of our preliminary analyses, during the GLMM analyses we assumed that feather hole abundance and clutch initiation dates fit a Poisson distribution and that each morphological and reproductive performance variable fit a Gaussian distribution. We used binomial distributions during GLMM analyses to examine whether there were relationships between (a) having 0 or ≥ 1 feather holes and morphology and reproductive perfor-mance; and (b) having bred only 1 time or ≥ 1 time at GVSU and feather hole abundance. We controlled for date in PROC GLIMMIX and specified the interaction between an individual (as indicated by its band number) and year as the random effect because (a) ASY females tend to have earlier dates of clutch initiation and larger clutch sizes, and to fledge more nestlings, than SY females (DeSteven 1978, Robertson and Rendell 2001); and (b) birds were most often captured when they were tending nestlings, such that individuals that bred earlier in the season were measured, and their feather holes counted, earlier in the season than those that bred later.

We report GLMM fixed-effects estimates to indicate the directionality (positive or negative) and degree of the effect of the independent variable(s) on the response variable(s) when GLMM analyses detected statistically significant relationships. All statistical tests were 2-tailed. Differences between measures were considered statistically significant if $P \leq 0.05$.

RESULTS

Feather Holes and Year

Mean feather hole abundance did not differ significantly among years for SY females (Kruskal-Wallis, $\chi^2_{12} = 17.95$, $P = 0.12$) but did for ASY females (Kruskal-Wallis, $\chi^2_{12} = 44.67$, $P < 0.001$) and males (Kruskal-Wallis, $\chi^2_{12} = 45.04$, $P < 0.001$). We did not control for year in subsequent analyses, however, because year contributed very little to the variation in mean feather hole abundance (SY females: $y = 399.23 - 0.19x$, $F_{1,\ 150} = 5.75$, $P = 0.62$, $r^2 = 0.002$; ASY
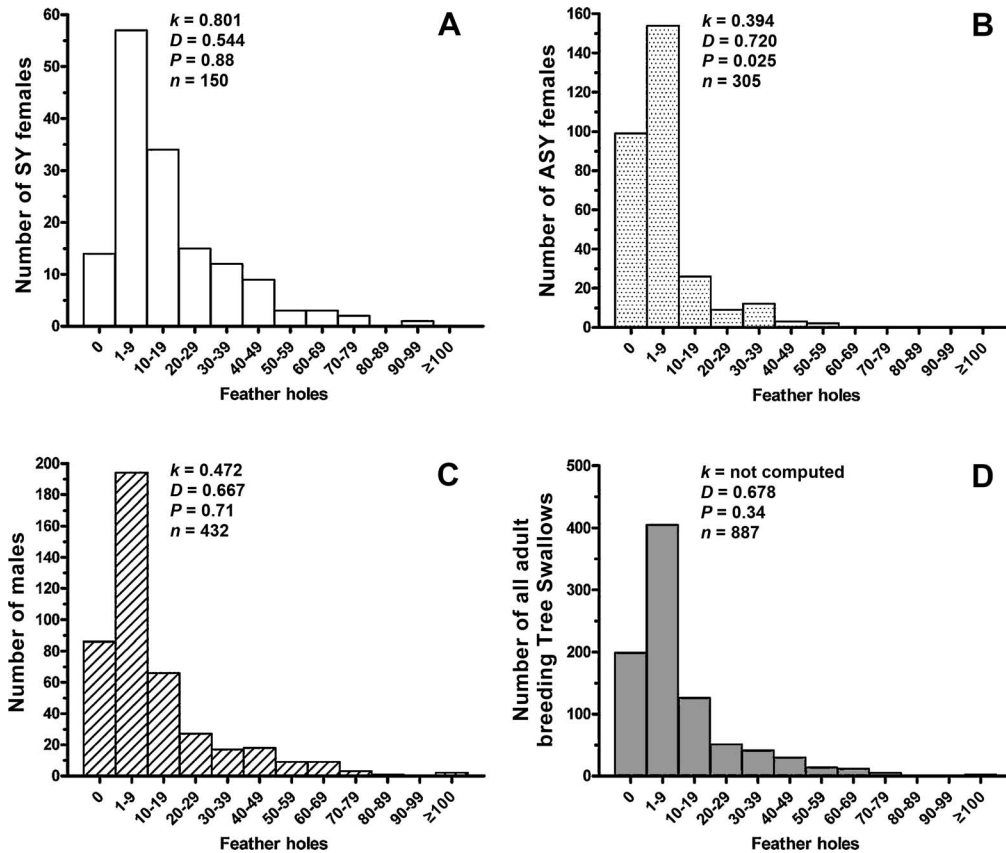
FIGURE 1. Distribution of feather holes by category of breeding Tree Swallows at the GVSU study site, Michigan, USA, 1993–2005. Measures of feather hole aggregation: k = index of aggregation (as the aggregation of feather holes increases, k approaches 0); and D = index of discrepancy, which quantifies aggregations as the discrepancy between the observed distribution and a hypothetical one in which all hosts are equally infected (D ranges from 0 [i.e. no aggregation] to 1 [i.e. all parasites are in 1 host]; Poulin 1993).

females: $y = 0.30x - 600.16$, $F_{1, 550} = 5.05$, $P = 0.03$, $r^2 = 0.009$; males: $y = 542.02 - 0.27x$, $F_{1, 650} = 2.24$, $P = 0.14$, $r^2 = 0.003$).

Feather Holes and Time of Year

When breeder category was accounted for, feather hole abundance increased significantly with date (GLMM, $F_{1, 1,220} = 24.98$, $P < 0.001$). However, the model was overdispersed (generalized chi-square test, df = 18.05), and date contributed a very small, but statistically significant, positive effect on feather hole abundance (GLMM, fixed-effects estimate, 0.0044 ± 0.0008 holes day^{-1}, $t_{1,220} = 5.00$, $P < 0.001$). When breeder categories were analyzed separately, feather hole abundance increased significantly with date only for ASY females (GLMM, $F_{1, 464} = 9.30$, $P = 0.002$). Again, the model was overdispersed (generalized chi-square test, df = 12.95). Similarly, whether or not we found ≥1 feather holes in a breeding individual increased significantly with date for ASY females (GLMM, $F_{1, 464} = 5.82$, $P = 0.02$; fixed-effects estimate, 0.0183 ± 0.008 ASY female day^{-1} with holes, $t_{461} = 2.41$, $P = 0.016$) but not for SY females or males (both $P \geq 0.28$).

Feather Holes and Breeding Swallow Category

Most breeding individuals had <10 holes in their wing and tail feathers (Figure 1). Distributions of feather holes for SY females and males did not differ significantly from those expected by the negative binomial distribution (i.e. they were aggregated; Figure 1). By contrast, the observed data for ASY females did not fit a negative binomial distribution, rendering k noninterpretable (Reiczigal and Rózsa 2005). We did not compute k for all birds pooled together because k values differed among breeder categories. Computing k for all birds pooled together would have resulted in a poorly fitted model (Wilson et al. 2002). Discrepancy values indicated a moderate level of aggregation of feather holes among individuals within each breeder category (Figure 1).

There were significant differences between breeder categories in feather hole prevalence (GLMM, binomial analysis; $F_{1, 1,220} = 8.87$, $P < 0.001$). The breeder categories differed significantly in mean (Fisher's exact test, $P < 0.001$) and median (Mood's median test, $P < 0.001$) prevalence; prevalence in SY females was greater than that in males and ASY females; males had greater prevalence than ASY females (all $P < 0.001$) (Table 1).

TABLE 1. Feather hole prevalence, intensity, and abundance in relation to breeder categories of Tree Swallows at the GVSU study site, Michigan, USA, 1993–2005. Prevalence (mean with 95% confidence interval [CI] in parentheses) is the percentage of all birds with ≥1 feather hole. Intensity (mean with 95% CI) is the number of feather holes in birds with ≥1 hole; birds with no feather holes were excluded from calculations of intensity. Abundance (mean ± SE) is the mean number of feather holes found in all birds, including those with no feather holes. Abbreviations: SY = second-year, ASY = after-second-year.

Breeder category	Feather hole prevalence	Feather hole intensity	Feather hole abundance
SY females ($n = 150$)	90.7 (8.48–94.8)	18.54 (15.9–21.9)	16.81 ± 0.47
ASY females ($n = 305$)	67.5 (62.0–77.3)	8.14 (6.85–9.88)	5.50 ± 0.55
All females ($n = 455$)	75.2 (70.9–79.1)	12.27 (10.8–14.0)	9.23 ± 0.66
Males ($n = 432$)	80.1 (75.7–83.8)	15.10 (13.4–17.3)	12.08 ± 0.85
All birds ($n = 887$)	77.6 (74.7–80.3)	13.69 (12.4–14.9)	10.60 ± 0.54

Mean (bootstrap 2-sample t-test, 1,000 replicates, $P < 0.0001$) and median (Mood's median test, $P < 0.0001$) intensity differed significantly among breeder categories and between SY and ASY females (both $P < 0.0001$) (Table 1). Likewise, mean intensity differed significantly between SY and ASY females pooled together and males (bootstrap 2-sample t-test, 1,000 replicates, $P = 0.02$), but median intensity did not (Mood's median test, $P = 0.12$) (Table 1).

Feather hole abundance differed significantly among SY females, ASY females, and males (Kruskal-Wallis, $\chi_2^2 = 85.07$, $P < 0.0001$); it was greater in SY than in ASY females (bootstrap 2-sample t-test, 1,000 replicates, $P < 0.0001$); greater in males than in SY and ASY females pooled together (bootstrap 2-sample t-test, 1,000 replicates, $P = 0.005$); greater in SY females than in males (bootstrap 2-sample t-test, 1,000 replicates, $P = 0.005$); and greater in males than in ASY females (bootstrap 2-sample t-test, 1,000 replicates, $P < 0.0001$) (Table 1).

Feather Hole Abundance and Morphology
When date was statistically accounted for, GLMM analyses did not detect significant associations between feather hole abundance and right tarsus (all $P \geq 0.16$), bill (all $P \geq 0.16$), or right tail fork (all $P \geq 0.21$) length within any breeder category. By contrast, feather hole abundance was negatively associated with mass ($F_{1, 549} = 5.12$, $P = 0.02$; GLMM fixed-effects estimate, -0.0066 ± 0.0029 holes g^{-1}, $t_{549} = -2.26$, $P = 0.02$) and right wing length in males ($F_{1, 550} = 5.56$, $P = 0.02$; GLMM fixed-effects estimate, -0.0175 ± 0.0074 holes mm^{-1}, $t_{550} = -2.36$, $P = 0.02$) but not in breeding SY or ASY females (both $P \geq 0.58$).

Feather Holes and Assortative Mating
Second-year females and their mates did not differ significantly in mean feather hole abundance (Figure 2), and linear regression analyses did not detect evidence of assortative mating based on feather hole abundance ($y = 16.57 - 0.03x$, $F_{1, 106} = 0.08$, $P = 0.78$, $r^2 = 0.001$). By contrast, ASY females had significantly fewer feather holes than their mates (Figure 2), and linear regression analysis revealed evidence of positive assortative mating based on feather hole abundance ($y = 0.09x + 5.65$, $F_{1, 448} = 5.75$, $P =$

0.02). However, the feather hole abundance in males explained very little of the variation in feather hole abundance in their ASY female mates ($r^2 = 0.01$). Males mated to SY females had significantly greater mean feather hole abundance than males mated to ASY females (Figure 2).

Feather Holes and Reproductive Performance
When date was accounted for, GLMM analyses did not detect significant associations between feather hole abundance and clutch initiation date (all $P \geq 0.20$), clutch size (all $P \geq 0.44$), or the number of fledglings produced (all $P \geq 0.42$) for any breeder category.
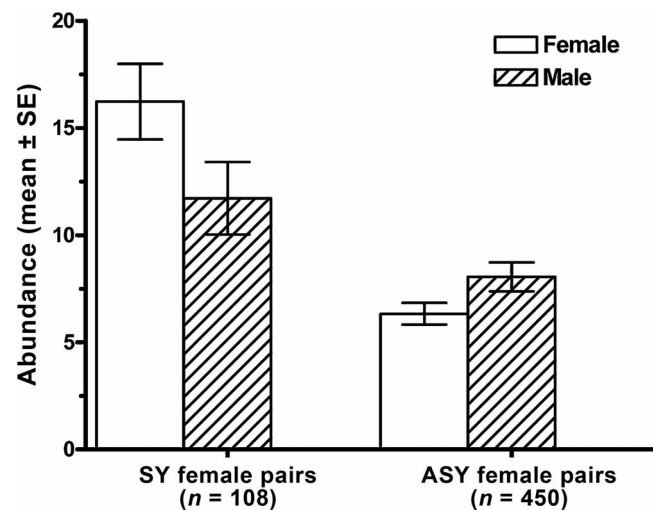
FIGURE 2. Comparisons of mean feather hole abundance between mates in Tree Swallows at the GVSU study site, Michigan, USA, 1993–2005. Mates in second-year (SY) female pairs did not differ significantly in mean abundance of feather holes (paired t-test, $t_{107} = 1.83$, $P = 0.07$). In after-second-year (ASY) female pairs, males had significantly more feather holes than their mates (paired t-test, $t_{449} = -2.16$, $P = 0.03$). Males mated to SY females had significantly greater mean feather hole abundance than males mated to ASY females (Mann-Whitney $U = 19,381.5$, $P = 0.001$).

TABLE 2. Presence or absence of feather holes in relation to whether a Tree Swallow bred only 1 time or >1 time at the GVSU study site, Michigan, USA, 1993–2005. Abbreviations: SY = second-year, ASY = after-second-year.

| Category of breeding bird	No feather holes		Feather holes present		χ_1^2	P
	Bred 1 time	Bred ≥2 times	Bred 1 time	Bred ≥2 times		
SY female	9	5	87	51	0.008	0.93
ASY female	63	105	126	254	0.972	0.32
Male	50	122	199	278	8.55	0.003

Feather Holes and Return Rates

When date was accounted for, feather hole abundance was significantly associated with whether males bred only 1 time or >1 time at GVSU (GLMM, $F_{1, 551} = 9.53$, $P = 0.002$), but not with whether SY or ASY females did so (both $P \geq 0.65$).

Breeding males, but not SY or ASY females, with no feather holes during their first breeding season at GVSU were more likely than males with ≥1 feather hole to breed ≥1 time (Table 2). However, within each breeder category, there were no significant differences in feather hole abundance during a bird's first breeding season between those individuals that bred only 1 time and those that returned to breed at least 1 more time at GVSU (all $P \geq 0.31$). However, mean feather hole abundance was significantly greater in the first than in the second breeding season for SY females and males, but significantly lower in the first than in the second season for ASY females at GVSU (Figure 3). Among birds that bred ≥4 times, there were no significant differences in feather hole abundance during an individual's first breeding season and subsequent breeding seasons for SY females, ASY females, and males (all $P \geq 0.18$). Mean feather hole abundance differed significantly among years for 12 SY females that bred 3 times, 17 ASY females that bred 4 times, and 17 males that bred 4 times at GVSU (Figure 4). In addition, mean feather
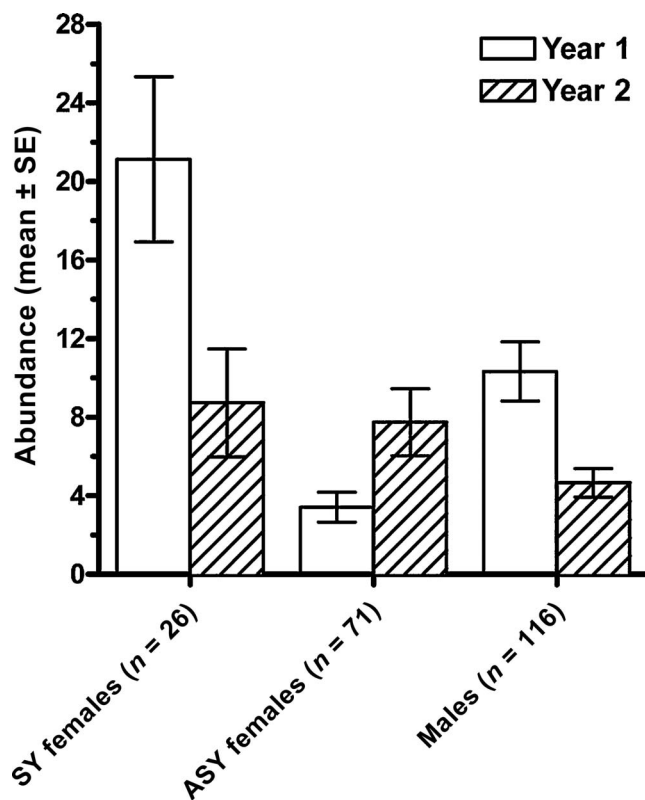
FIGURE 3. Comparisons of mean feather hole abundance for each breeder category in first- and second-year breeding Tree Swallows at the GVSU study site, Michigan, USA, 1993–2005. There were significant differences in mean feather hole abundance between first- and second-year breeding for second-year (SY) females (paired t-test, $t_{25} = 3.00$, $P = 0.006$), after-second-year (ASY) females (paired t-test, $t_{70} = -2.30$, $P = 0.02$), and males (paired t-test, $t_{115} = 3.42$, $P = 0.001$).
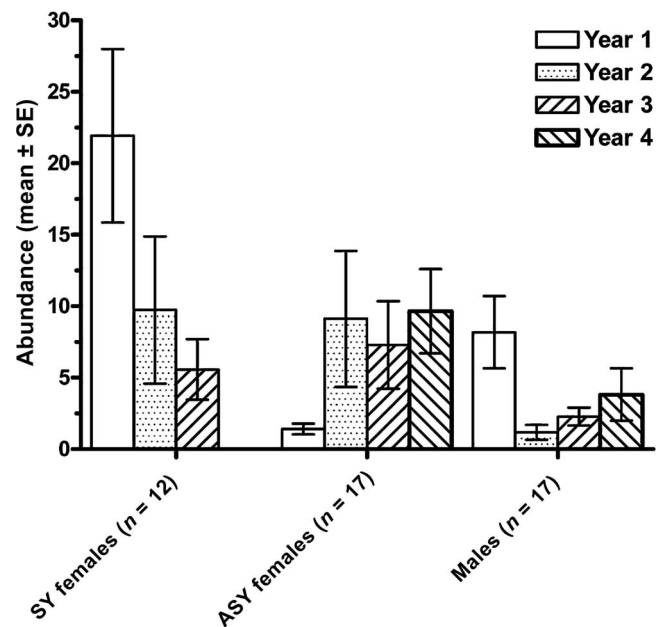
FIGURE 4. Comparisons of mean feather hole abundance for each breeder category in first-, second-, third-, and fourth-year breeding Tree Swallows at the GVSU study site, Michigan, USA, 1993–2005. Feather hole abundance differed significantly among years for 12 second-year (SY) females that bred 3 times ($F_{1, 11} = 12.41$, $P = 0.005$), 17 after-second-year (ASY) females that bred 4 times ($F_{1, 16} = 11.69$, $P = 0.004$), and 17 males that bred 4 times ($F_{1, 16} = 14.92$, $P = 0.001$).

hole abundance significantly differed among years for 11 males that bred 5 times at GVSU ($F_{1, 10} = 11.53$, $P = 0.007$).

DISCUSSION

The pattern of feather hole aggregation we observed in breeding Tree Swallows was typical of the macroparasite aggregations found in other vertebrate hosts (Shaw and Dobson 1995, Shaw et al. 1998). Most individuals had <10 feather holes; only a few had many. Indices of discrepancy for all categories indicated a moderate level of aggregation of feather holes among individuals in each breeder category.

Depending on breeder category, feather hole prevalence ranged from 68% to 90%. These prevalence values are lower than those reported for Barn Swallows in separate studies in Hungary: >99% of 673 adult females and males in eastern Hungary (Pap et al. 2005) and 88–97% of 781 adults and juveniles at 2 locations in central Hungary had feather holes (Vas et al. 2008). A lower prevalence, 52% of 25 adult Barn Swallows, was observed in Spain (Barbosa et al. 2002). Shutler et al. (2004) found that 46% of 52 adult Tree Swallows sampled in Saskatchewan, Canada, had lice of the genera *Brueelia* and *Myrsidea*. *Myrsidea* (Suborder Ambylcera) feed by chewing on skin and so are not responsible for producing feather holes (Johnson and Clayton 2003). *Brueelia longa* were much less prevalent on Cliff Swallows (*Petrochelidon pyrrhonota*) than on either Barn or Tree Swallows; only 8% of 1,551 Cliff Swallows breeding in western Nebraska harbored *B. longa* (Brown et al. 1995). Variations in prevalence among different swallow species suggest that they vary in their susceptibility to infestations of feather-chewing lice, and different populations of the same species exhibit geographic variation in prevalence. Differences among populations in prevalence could also result from differences among observers in their louse-detection abilities. It is not surprising that colonially nesting Barn Swallows (Brown and Brown 1999), on average, had a higher prevalence of feather holes than Tree Swallows, because lice tend to be more prevalent and less aggregated on colonial than on territorial hosts because lice typically require body-to-body contact for transmission (Rékási et al. 1997). It is surprising that ischnoceran lice infested relatively few colonially nesting Cliff Swallows that often build their nests in contact with one another because other ectoparasites frequently infest Cliff Swallows (Brown and Brown 1996).

In the present study, feather hole prevalence and abundance varied significantly among categories of breeding Tree Swallows and were lowest in ASY females, followed by males and SY females. This pattern suggests that ASY female Tree Swallows may be more resistant than males and SY females to ischnoceran infestations.

Because feather-chewing lice rely primarily on physical contact between hosts for dispersal opportunities, Brooke (2010) predicted that lice would preferentially aggregate on female, rather than male, Eurasian Blackbirds (*Turdus merula*) to increase their chances of dispersal to new hosts because females brood nestlings more than males do. He found that prevalence, but not intensity, of *Brueelia merulensis* was greater on females than on males but did not detect differences between male and females for 2 other species of feather lice, *Philopterus turdi* and *Menacanthus eurysternus* (Brooke 2010). Similarly, Potti and Merino (1995) found that the ischnoceran lice *Docophorulus capillatus* were more prevalent and abundant on female than on male Pied Flycatchers (*Ficedula hypoleuca*). By contrast, feather hole prevalence and mean abundance were significantly lower on female than on male Tree Swallows, even though opportunities for louse dispersal are greater from females to nestlings because females brood and feed nestlings more often than males do (Lombardo 1991, Winkler et al. 2011). Others have not found sex-related patterns of ectoparasite infestations, for example in Barn Swallows (Pap et al. 2005, Vas et al. 2008) and House Sparrows (*Passer domesticus*; Moreno-Rueda 2010). Collectively, these results indicate that sex-related patterns of ectoparasite infestation vary among passerine species.

Similarities in feather hole abundance between mates may reflect positive assortative mating or, more simply, recent transmission of lice from a mate. For example, Potti and Merino (1995) found a significant correlation between Pied Flycatcher mates in the number of *D. capillatus* lice on their crowns. By contrast, in the present study, although SY female Tree Swallows and their mates did not differ in mean feather hole abundance, there was no correlation between mates in abundance—a pattern inconsistent with assortative mating. The significant correlation between ASY females and their mates in feather hole abundance is consistent with both assortative mating and recent transmission of lice between mates. However, the observation that ASY females had significantly fewer feather holes than their mates (Figure 2) is inconsistent with the "recent transmission" explanation, reinforcing the hypothesis that ASY females are more resistant to infestations of chewing lice than other categories of breeding Tree Swallows. Additionally, the mates of ASY females had significantly fewer feather holes than the mates of SY females. This pattern suggests that older males may be more resistant than younger males to ischnoceran infestations because the mates of SY females are more likely to be younger than the mates of ASY females (Robertson et al. 1992).

The overall pattern of younger individuals having greater feather hole prevalence and abundance than older ones suggests 2 explanations that are not mutually exclusive. First, perhaps older birds become more resistant to feather-chewing lice because, with experience, they

become better at mechanically removing lice from their feathers (Clayton et al. 2010). Alternatively, older birds, as a result of their prior experience, may have more time available for removing ectoparasites because they take less time to perform other tasks such as nest building and foraging. Second, it is also possible that decreasing prevalence with age may result from the feathers of older individuals being less palatable or digestible to lice (Johnson and Clayton 2003, D. Shutler personal communication). Finally, young individuals with large numbers of feather holes may be of lower overall quality and do not survive. However, our data suggest that feather hole abundance—and, thus, the ability to resist damage from feather-chewing lice—had little effect on the survival of breeding Tree Swallows.

The patterns of aggregations of feather holes that we observed suggest that feather-chewing lice may not typically be important causes of selection in Tree Swallows, in that a small proportion of individuals had many feather holes (Figure 1). Consequently, if there is parasite-associated mortality, a small proportion of the host population would be lost, and a large segment of the parasite population would be lost simultaneously (Poulin 1993, Wilson et al. 2002). Indeed, observations suggest that lice are weak causes of selection in wild birds under most circumstances (Rékási et al. 1997). For example, feather-chewing lice had little direct effect on their hosts during the breeding season in Rock Pigeons (*Columba livia*; Clayton and Tompkins 1995) and Common Swifts (*Apus apus*; Lee and Clayton 1995, Tompkins et al. 1996; but see Booth et al. 1993). For several additional reasons, we think that feather-chewing lice had little effect on the evolutionary fitness of Tree Swallows breeding at GVSU during our study period, and we therefore conclude that they may not typically be an important cause of selection in this species.

First, although feather hole abundance increased with date for each breeder category, the effect of date was small. The overdispersion of the model describing the relationship between date and feather hole abundance suggests that unmeasured factors influenced the increase in feather holes with date (Crawley 2002). In addition, the abundance of feather holes found on SY females and males, but not ASY females, over the course of the breeding season was not influenced significantly by date. Moreover, the overdispersion of the model describing the relationship between date and feather hole abundance in ASY females suggests that unmeasured factors influenced the increase in feather holes in these Tree Swallows as the season progressed (Crawley 2002). Taken together, these results suggest that feather-chewing louse infestations on individuals do not change appreciably over the course of a breeding season. Although this hypothesis requires a direct test, the pattern suggests that Tree Swallows may become

infested with feather-chewing lice before the breeding season commences and control louse infestations as the season progresses, thereby limiting feather damage. Alternatively, as feathers grow and harden after molting, they may become more difficult for lice to chew and, therefore, more resistant to damage (Johnson and Clayton 2003). This hypothesis needs experimental testing. Because Tree Swallows molt their flight feathers before migrating south (Dwight 1900, Stutchbury and Rohwer 1990), the consequences of feather holes on long-distance flying ability during the southward migration are probably low. By contrast, feather hole number increased on recaptured Barn Swallows over the course of the season in Hungary, which suggests that those birds did not limit damage to their feathers caused by feather-chewing lice (Vas et al. 2008). In one study, there was little association between cell-mediated immune responses and richness of ischnoceran genera in Barn Swallows, which suggests that avian immune systems may not be able to control ischnoceran lice (Møller and Rózsa 2005). Swallows probably use their bills to mechanically remove lice from feather shafts (Clayton et al. 2010), although lice may avoid being removed by "hiding" between feather barbs (Vas et al. 2008).

Second, we found no significant associations between feather hole abundance and measures of Tree Swallow reproductive performance. By contrast, feather hole abundance was negatively correlated with arrival times on breeding grounds (Møller et al. 2004) and positively correlated with delayed onset of breeding in Barn Swallows (Pap et al. 2005). However, as in Tree Swallows, feather hole abundance in Barn Swallows was not significantly associated with clutch size or breeding success as measured by the number of fledglings produced. Moreover, feather hole abundance was not associated with nestling condition or patterns of male and female parental care in Barn Swallows (Pap et al. 2005). We did not examine relationships between feather hole abundance and nestling condition or patterns of parental care in Tree Swallows.

Third, feather hole abundance had little effect on Tree Swallow return rates. It did not significantly affect whether SY or ASY females bred >1 time at GVSU. By contrast, males with more feather holes were less likely to breed >1 time. However, there were no significant differences in mean feather abundance during the first breeding season of individuals that bred 1 time or >1 time. This suggests that feather holes had little effect on survivorship, because Tree Swallows show breeding-site fidelity (Winkler et al. 2004). Similarly, there was not a relationship between louse prevalence and Pied Flycatcher survival (Potti and Merino 1995). By contrast, feather holes and ectoparasite loads have been associated with decreased survivorship in Cliff

Swallows (Brown et al. 1995) and Barn Swallows (Pap et al. 2005).

Mean feather hole abundance significantly differed among years for Tree Swallows that bred multiple times at GVSU. Both SY females and males had fewer feather holes after their first breeding season, which suggests that, over time, they became more resistant to feather damage caused by feather-chewing lice. However, this explanation makes it unclear why feather hole abundance increased in ASY females after their first breeding season. By contrast, Pied Flycatchers of both sexes had similar louse loads in successive years, which suggests no improvement in their ability to control louse infestations with experience (Potti and Merino 1995).

Finally, there were few significant associations between feather hole abundance and morphology in breeding Tree Swallows, which suggests little interaction between the ability to resist feather damage from feather-chewing lice and body size. Male Tree Swallows with relatively few feather holes weighed more and had longer right wings than those with more feather holes. These observations suggest a possible link between the ability to resist damage from feather-chewing lice and typical measures of physical quality in birds. In Barn Swallows, Barbosa et al. (2002) found no significant relationships between feather hole abundance and wingspan or tail length, but Pap et al. (2005) found that males with more feather holes had shorter tail feathers. Potti and Merino (1995) found a negative correlation between louse load and body condition in Pied Flycatchers. Collectively, these results suggest variation in the association between feather-chewing louse infestations and body condition both within and among passerines.

In summary, ischnoceran louse infestations, as estimated by the prevalence and abundance of feather holes, appeared to have little effect on the evolutionary fitness of Tree Swallows nesting at GVSU. In retrospect, this result is not surprising because other evidence suggests that events during the breeding season may not be important causes of selection in this species under most circumstances. First, reproduction, as estimated by the return rates of breeders, appears to be relatively "cost-free" in Tree Swallows (DeSteven 1980, Wiggins 1990, Wheelwright et al. 1991, Murphy et al. 2000, Shutler et al. 2006), and local experience has little effect on subsequent reproductive performance (Lombardo and Thorpe 2010). There is no compelling evidence that feather mites (Shutler et al. 2004), parasitic worms (Winkler et al. 2011), blood parasites (Shutler et al. 2004, Szymanski and Lovette 2005, M. P. Lombardo personal observation), or cloacal and semen microbes (Lombardo et al. 1996, Lombardo and Thorpe 2000) negatively affect adult survivorship or reproductive success, although they must under some circumstances. These observations suggest

that, on average, breeding Tree Swallows are in good physical condition.

Finally, we propose that it should not be surprising that breeding Tree Swallows appear to be in good physical condition, because a Tree Swallow breeding "colony" is, in a sense, like an Olympic Village. Just as all of the inhabitants of an Olympic Village are of superior quality compared with the nonqualifying athletes they outcompeted during several rounds of preliminary competitive events, breeding Tree Swallows have also successfully made it through their "preliminary events." Breeding Tree Swallows have survived migration between breeding areas and overwintering grounds and successfully competed in nest-site and mate acquisition; ceteris paribus, individuals of inferior quality failed at these "events." Consequently, just as there are few significant physical differences among athletes competing in the same Olympic events (Uth 2005), there are likely to be few physical differences between breeding Tree Swallows. In the context of our study, perhaps those individuals most susceptible to feather damage from feather-chewing lice did not become breeders and therefore were not sampled. Consequently, the differences we detected in the effects of feather-chewing lice among our sample of breeding Tree Swallows were small. This perspective implies that natural selection may be more intense during the migration and overwintering phases of the Tree Swallow's life cycle than during the breeding season. We suggest that this may also be the case for other migratory, secondary cavity-nesting birds that migrate long distances between overwintering and breeding grounds and compete for limited nest sites (von Haartman 1957).

ACKNOWLEDGMENTS

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