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Seasonal plumage condition variation and the thermal value of the feather coats of house sparrows (*Passer domesticus*)

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**Seasonal Plumage Condition Variation and the Thermal Value of the Feather Coats of
House Sparrows (*Passer domesticus*)**

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Honors Thesis

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Introduction

Feathers are the defining taxonomic characteristic of birds and serve many functions including flight, communication, and crucially, insulation (Morris 1956). Birds have the highest average internal body temperatures of any vertebrate group, with most birds operating at 40-44°C. Thus, their feathers are a vital part of their energy balance, especially in cold environments, where defending their high core temperature is difficult (Wetmore 1921, McNab 1966). Despite the clear importance of feathers, the majority of the literature on thermal flux in birds has focused on metabolic differences within individuals (Brush 1965), within seasons (Brush 1965, Arens and Cooper 2005, Hart 1962, Veghte 1964, Dawson and Carey 1976, Cooper and Swanson 1994, Bush et al. 2008, Nzama et al. 2010, Noakes et al. 2016), and among species (Hart 1962, Weathers 1981, Londoño et al. 2015, Pollock et al. 2019) while largely ignoring the role of feathers themselves in insulation.

Feathers insulate birds by trapping warm, still air beneath the surface of the feathers, creating a physical barrier to heat loss (Lucas and Stettenheim 1972). Feathers are composed of a central shaft, called a rachis, with lateral projections called barbs (Lucas and Stettenheim 1972). Generally, there are two types of barbs: pennaceous and plumulaceous (Lucas and Stettenheim 1972). These barb types are differentiated by the morphology of their barbules, which are hooked, lateral projections off the barbs. Pennaceous barbs have many barbules which cause the barbs to lock together tightly and form a stiff vane of feathering, whereas plumulaceous barbs have fewer barbules, so barbs do not interlock and instead form a loose, “fluffy” mass of barbs over the skin (Lucas and Stettenheim 1972). Contour feathers have a pennaceous distal portion and plumulaceous proximal portion of barbs (Lucas and Stettenheim 1972). The pennaceous

portion of contour feathers forms the body covering and prevents insulative air from escaping the feather coat, while the plumulaceous portion creates air pockets (Lucas and Stettenheim 1972).

A number of investigators have found seasonal variation in the feather coat, with more feathers in the winter than in the summer in some species (Wetmore 1936, Staebler 1941, Barnett 1970). Wetmore (1936) counted the total number of contour feathers of 152 birds of 79 Eastern North American species collected from February to October and found significant seasonal variation, with a maximum number of feathers in the winter, steadily declining to a minimum number of feathers in the summer. Staebler (1941) claimed that house sparrows (*Passer domesticus*) show an 11.5% difference in the number of feathers between seasons, and Barnett (1970) found a staggering 70% difference in the weight of house sparrow feathers between August and October. Both of these results are surprising because house sparrows only molt once per year (Lowther and Cink 1992), so the number of feathers should not change seasonally. However, feathers may be lost from activities such as grooming, plucking, fighting, or other activities that pull at feathers (Howell 2010).

Wear might also explain the change in the weight of the feather coat. Feather wear damages or removes barbs and barbules from friction with large objects such as grass and branches and smaller objects such as airborne particles, or from repeated bending (Burt 1986). Willoughby (1986) showed that feather wear slowly increased from January to August and then decreased from September to December during the molt of Cassin's and Bachman's Sparrows (*Aimophila cassinii* and *A. aestivalis*). Wetmore (1921) noticed that in the summer, feathers become thinner, more worn, and less numerous than winter feathers.

While these overall patterns are consistent, many studies investigating the effect of feather structure on thermal insulation are conflicting. Several studies have shown that birds

living in colder climates have more extensive plumulaceous portions of contour feathers than birds living in warmer climates (Lei et al. 2002, Pap et al. 2017). Additionally, Middleton (1986) showed that freshly molted contour feathers from winter American goldfinches (*Carduelis tristis*), which molt twice a year, had a higher proportion of plumulaceous barbs than freshly molted contour feathers from summer birds, and hypothesized that this was an adaptation to the thermal differences between seasons. Conversely, Broggi et al. (2011) studied two captive outdoor populations of great tits (*Parus major L.*) and found that the more northern population had a denser plumage (i.e. more feathers per unit area) made of shorter contour feathers with, counterintuitively, a *shorter* plumulaceous portion, whereas the more southern population had a less dense plumage with longer feathers with a longer plumulaceous portion. This suggests that perhaps the density of feathers is more important to insulation than feather length or composition.

Despite the extensive research on how feathers vary, very few attempts to directly quantify how this variation affects the thermal insulation of birds have been made (but see Taylor 1986, Novoa et al. 1994, Ward et al. 2001 and 2007). Novoa et al. 1994 measured thermal conductance in dead birds in summer and winter with and without plumage to quantify thermal conductance. They found that conductance increased in feathered birds in summer, indicating a decrease in insulation over the course of the year, as well as a ~2.5 times increase in thermal conductance in defeathered birds, suggesting that the feather coat itself provides a significant amount of insulation (Novoa et al. 1994).

In this study, we used house sparrows to directly measure the thermal value of the feather coat both holistically using live birds and, in order to isolate and measure the thermal contribution of the feather coat itself, using skins of the same birds, alone. As a common, widely

distributed, invasive species, house sparrows are readily available and have demonstrated the ability to adapt to new climates, thus making their thermal biology of particular interest.

We investigated how plumage condition affects passive heat loss in birds by comparing the thermal values of feathers between winter and summer house sparrows. We compared the surface temperature of live birds to that of their own flat-skins in order to isolate the thermal value of the feather coat, alone, from other thermal strategies used by live birds such as fat, behavioral thermoregulation (Cook et al. 2020, Pessato et al. 2020), and physiological acclimation (Brush 1965, Arens and Cooper 2005, Hart 1962, Veghte 1964, Dawson and Carey 1976, Cooper and Swanson 1994, Bush et al. 2008, Nzama et al. 2010, Noakes et al. 2016). We hypothesized that feathers would be more worn in summer than in winter, and thus, both live birds and their feather coats collected in the summer should passively lose more heat than birds collected in the winter. We also hypothesized that within individuals, the thermal performance of the feather coat alone would be less than that of a living bird because live birds have several other methods of thermoregulation available to them; thus, the feather coat alone should passively lose more heat than a feather coat on a living bird.

Methods

Field Collection:

We trapped house sparrows on the campus of the University of Connecticut in 2019 and early 2020 (IACUC Protocol No. A19-023). We retained and used only male house sparrows because house sparrow juveniles and females are indistinguishable, whereas males have a distinct plumage pattern (Lowther and Cink 1992). Collecting only males ensured that all of our specimens were adults and that any differences in insulation were not due to young age. House sparrows molt once a year, starting in August and finishing in October (Lowther and Cink 1992).

Therefore, our data are all drawn from 1) “winter” house sparrows, collected in the months from November 1st to March 1st, when molt has just been completed and feathers should be new and unworn; and 2) “summer” house sparrows, collected in July, just before molt begins, and feathers should be old, and at their most worn. We trapped house sparrows using mist nets from July 22nd, 2019 to August 2nd, 2019 for our summer sample, and again from November 16th, 2019 to February 9th, 2020 for our winter sample. We netted both inside, and in the area around the outside of, the semi-open Cattle Resource Unit at Horsebarn Hill on the University of Connecticut campus in Storrs, CT. A single bird was caught at another suburban location about five miles away in Storrs. We achieved a sample size of 19 birds in the summer sample and 9 birds in the winter sample. Winter trapping was much more difficult and less successful; in the summer, birds frequently flew to the ground to eat scattered cattle feed, and they roosted in the barn overnight because they had nests there. In the winter, birds frequented the barn during the day, but roosted elsewhere. Additionally, birds seldom moved around on the ground in the winter; they stayed up in the rafters.

We released all females, juveniles, and non-target species immediately after removal from mist nets. If we caught more than one male at a time, we held these surplus males in small, darkened holding cages with access to food and water. We held all birds for less than 4 hours, in total, including their time in the environmental chamber.

Thermal Measurements of Live Birds:

We created an environmental chamber by modifying a myTemp™ Mini H2200-HC digital incubator in order to record thermal videos (FLIR SC655, 680 x 480 px resolution, $\pm 2^{\circ}\text{C}$ or $\pm 2\%$ accuracy) of each bird across a range of ambient temperatures from 16-38°C. We chose this range because it encompasses and slightly exceeds the largest estimate of thermoneutral

zone of house sparrows, which is 21-37°C (Kendeigh 1969). Because thermal cameras cannot record temperatures through surfaces such as plexiglass, we cut a hole through the front of the door directly in front of the perch and added an insulated foam tubular viewing port to house the camera lens at the minimum focusing distance of the thermal camera (.4 m) (Fig. 1). This allowed us to film birds with no physical barrier between the lens of the thermal camera and the bird.

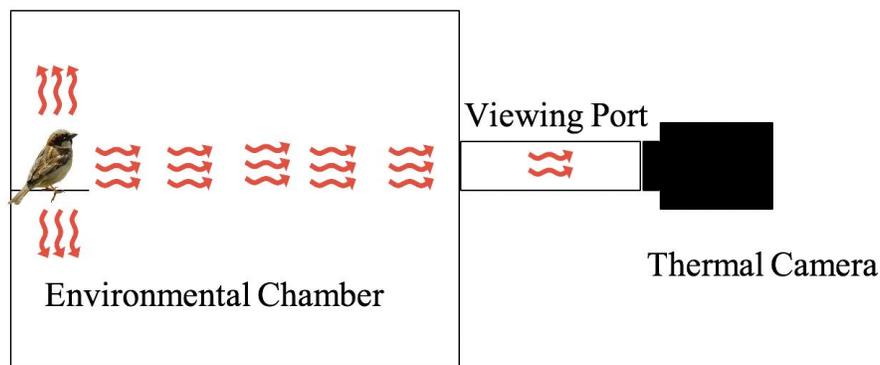


Figure 1: Diagram of the field experiment set up.

In initial attempts, birds were very inclined to explore the environmental chamber, which slowed the experiment as birds got off the perch repeatedly. We modified the chamber several times until the perch was contained within a wire sphere which was open to the viewing port so the bird was not obscured by any material, and remained within the focal distance of the camera.

With the chamber set at 16°C, we placed each bird in the chamber and waited for it to settle on the perch. We waited five minutes before we began taking thermal videos of the bird to let the bird acclimate to the ambient temperature. We recorded the bird in two positions: with the bird looking straight forward and with its head in profile. After recording, we increased the temperature in the chamber by 2°C. We allowed two minutes for the chamber to come to

temperature and five minutes for the bird to acclimate to the new temperature (a total of seven minutes) before taking more thermal videos. We continued this process until the chamber reached 38°C. At that point, we removed the bird from the chamber, euthanized it immediately, and placed it in a freezer.

If the bird refused to settle on the perch within 30 minutes and we failed to record any thermal videos of it, we released it. On two occasions, when there were a limited number of birds left in the area, we sacrificed birds which refused to settle to skin and use in thermal measurements of the feather coat at a later time. If the bird got off of the perch during the experiment, we waited for the bird to settle and then waited five minutes before resuming filming with the thermal camera. If the bird got off of the perch during the experiment and did not settle on the perch again within 30 minutes, we removed the bird from the chamber and immediately euthanized it.

Using FLIR ResearchIR Max (v4.40.7.26, 64-bit) software, we measured the surface temperature of birds in five regions: the center of the eye, the top of the head in profile, the top of the head in front view, the breast, and the beak (Fig. 2). We measured the temperature of all areas except for the beak at a single pixel; we defined the temperature of the beak by the mean temperature of the total area of the beak. We standardized our methods for gaining repeatable landmarks (Fig. 2): first, we drew a circle around the eye in the software. Next, we drew a straight line which passed through the tip of the beak and the center of the eye. We added a line parallel to this line and drew it to pass through the most distal point of the wrist joint. We then drew a line perpendicular to these which also passed through the center of the eye. The intersection between this line and the line which passed through the wrist was defined as the breast. We measured the top of the head in profile on this perpendicular line a few pixels down

from where the feathering ended. We measured the top of the head in front view by drawing a line straight through the tip of the beak and the center of the feathering at the most proximal border of the culmen and then taking a point a few pixels down from the where the feathering ended at the top of the head. We measured the breast in profile rather than front view because the bird was not often fully facing the camera for the front view shot; it merely turned its head toward the camera. JG chose which frame gave the clearest view of each of these measurement areas and recorded the temperature of each area at each ambient temperature value.

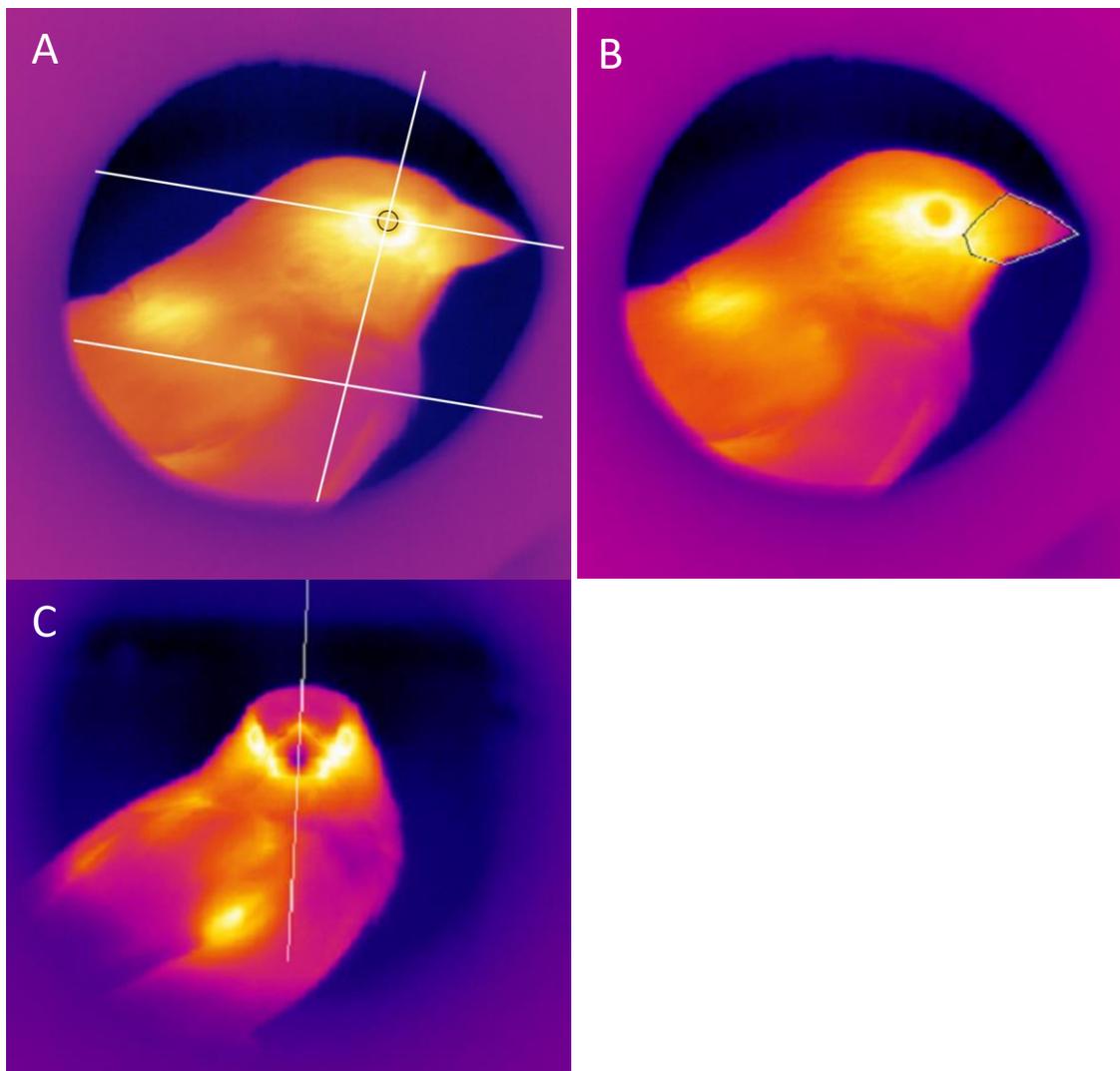


Figure 2: Measurement areas of a) the eye, the side of the head, and the breast, b) the beak, and c) the head in front view of live birds in the thermal software.

Thermal Measurements of the Feather Coat:

We measured heat loss through the feather coat on flat-skins prepared from the bodies of birds measured in the environmental chamber, in order to isolate and measure the insulation value of the feather coat alone, by removing factors present in live birds such as physiological acclimation, behavioral thermoregulation, and fat. To reduce error on all measurements, JG prepared and measured all specimens as flat-skins according to Spaw's (1989) protocol. Using the method detailed in Graveley et al. (2020), we measured the amount of heat which escapes through the flat-skin and feathers of each house sparrow. We used a constant temperature hot water bath set to 40°C (mimicking the internal temperature of a living house sparrow, Wetmore 1921, McNab 1966) capped with a sheet of plexiglass to supply a standard, continuous supply of heat. The plexiglass allowed heat, but not water, to rise off the surface of the bath in order to keep the flat-skin from getting wet. Above the plexiglass was a sheet of foam with a ½ inch diameter hole through it, over which we placed the flat-skin, skin side down. This arrangement places the skin over a controlled point of heat, so that only a precise area of the flat-skin is exposed to the heat and therefore allowing us to obtain a comparable, replicable value for every bird. Using a FLIR SC655 thermal camera, we quantified temperature values at the surface of the feather coat above the point source of the heat (Graveley et al. 2020).

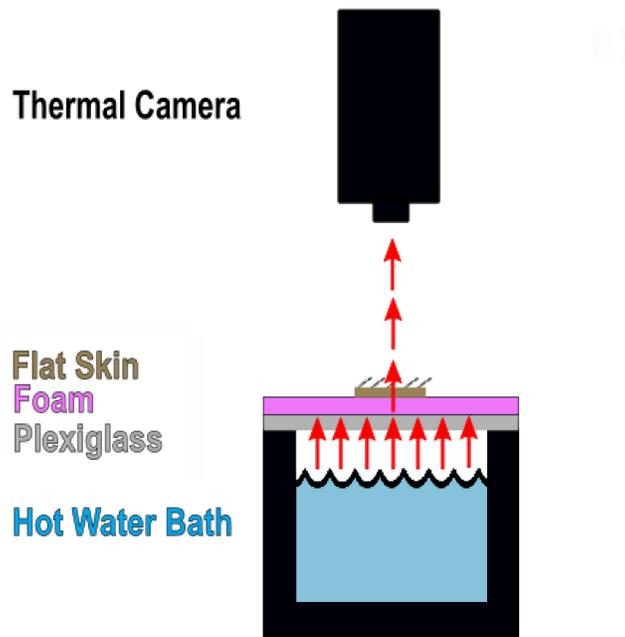


Figure 3: Set up for measurements of the feather coat (reproduced from Graveley et al. 2020)

In order to contain inter-observer handling error, only one of us (JG) measured flat-skins. In order to make thermal measurements of the feather coat alone comparable to the breast area measured in the live thermal measurements, the upper right-hand side of the bird's breast was placed over the heat source. On flat-skins, this area is not obstructed by other parts of the body such as the wing, and is least subject to edge effects. The head section of the skin, for example, has a small surface area and is subject to heat loss around the edges if placed over the heat source. After placing the skin on the foam, JG waited 30 minutes to allow the temperature of the skin to stabilize before taking a thermal image; the temperature at a single pixel in the measurement area was recorded. Immediately thereafter, JG lifted the flat-skin and took a thermal image of the plexiglass, recording the temperature at the same pixel, in order to get an

accurate reading of the temperature the skin was exposed to, before replacing the skin and repeating the wait period and thermal measurement five times. We repeated the measurement on each skin 5 times, to account for placement variation; we report and analyze here means of repeated measures for each bird. To compare the feather coat insulative differences between seasons, we analyzed the data using a generalized linear mixed model in the R package “nmlme” version 3.1-152 (Pinheiro et al. 2021), with bird ID added as a random effect to account for the individual variation of each bird.

Feather Wear:

We measured feather wear on individual contour feathers. Contour feathers were removed from the area of breast from which thermal measurements were taken in the live experiment, as close to the calamus as possible. After removal, feathers were stored individually in dry plastic Ziploc bags labeled with letters corresponding to the bird they came from. This ensured that the person measuring wear was blind with respect to knowing which feathers came from summer or winter birds. Pap et al. (2017) showed that storage in Ziploc bags poses no threat of feather deterioration. If we accidentally pulled multiple feathers from one bird, we labeled them with the relevant letter plus a number (e.g., “A1”, “A2”, and so forth). JG pulled and labeled all feathers; in order to reduce observer error, a single research assistant measured the feather wear. Feather wear was measured using a stereo microscope (Olympus SZ51) at a magnification (10x) which allowed the entire feather to be seen within the eyepiece, yet still made it possible to see and count individual barbs on each feather. Using forceps and a probe to manipulate the feather and barbs, we counted the total number of broken barbs along the complete length of each feather, on both sides of the rachis. We considered a barb broken if any part of its length was missing. We did not consider broken barbules in this count if it did not

affect the overall length of the barb, i.e., if only the barbule and not the barb was broken. When counting barbs for wear, we considered any barb with any plumulaceous barbules along its length a plumulaceous barb, and any barb with only pennaceous barbules along its length was considered a pennaceous barb (Butler et al. 2008). Pennaceous barbules are stiff and filled with tertiary interlocking projections called hooklets, whereas plumulaceous barbules interlock less and lack hooklets (Lucas and Stettenheim 1972).

We used a hand counter to record the numbers of barbs, counting each barb and listing it as plumulaceous or pennaceous and broken or not broken. It was sometimes necessary to use a microscope slide to view the feather if the feather would not lie flat enough to view effectively, or if the feather would not remain still on the microscope platform. In such a case, we gently laid a clear, clean microscope slide over the feather, and manipulated the feather under the slide with the probe when necessary by lifting the slide.

In the few cases that multiple feathers were pulled from one bird, we averaged the data from those feathers so each bird was only represented once. We only included counts from whole feathers in the analysis.

Results

Feather Wear:

As expected, feathers had significantly more broken barbs in summer than in winter (Fig. 4). This was true of all barbs (Fig. 4a, $p = 0.00002$), as well as pennaceous (Fig. 4b, $p = 0.0002$) and plumulaceous (Fig. 4c, $p = 0.0002$) classes of barbs. Beyond these significant increases in wear in the summer, several interesting patterns emerge. First, the median value of broken to non-broken barbs nearly doubled from winter to summer in both pennaceous and plumulaceous

barbs, so these differences are large. Second, the amount of variance in feather wear is much greater for pennaceous barbs than it is for plumulaceous barbs in the winter, and the ratio of broken plumulaceous barbs in the winter is still relatively high (Fig 4b). This is likely because pennaceous barbs are on the distal end of the feather, so they are more exposed to potential sources of breakage. Thus, even in the winter, some birds had high ratios of broken pennaceous barbs. Additionally, all barb types had some amount of wear even in the winter, suggesting that wear begins quickly after molt.

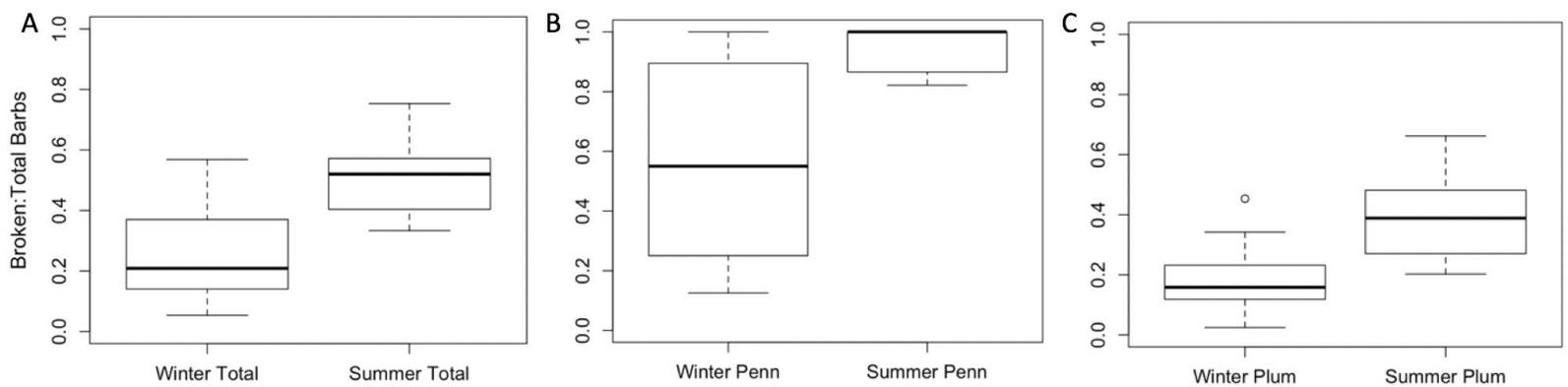


Figure 4: The ratios of broken to total a) barbs of all kind, b) pennaceous barbs, and c) plumulaceous barbs according to season.

Thermal Measurements of Live Birds:

We found no significant differences among thermal measurements of live birds between seasons in any body area (Fig. 5). Ambient temperature explained nearly all of the variation in the temperature at the breast for both summer ($R^2 = .9687$) and winter ($R^2 = .9307$) birds (Fig. 5a). Surface temperature at both regions of the head followed a similar pattern to that of the breast (Fig. 5b and 5c), in that the temperatures at the surface of the feather coats on the head were similar to those on the breast, and did not differ significantly between seasons. Variation in the mean temperature of the beak was greater than that of the breast or head, and beak

temperature is significantly and positively correlated with ambient temperature (Fig. 5d). Finally, eye temperature was not well explained by ambient temperature in either summer ($R^2 = .6051$) or winter ($R^2 = .5908$) birds, and we did not find significant differences in eye temperature between seasons (Fig. 5e).

For the breast and the head, feather coat temperature was about equal to ambient temperature (Fig. 5a, 5b, 5c), suggesting that the feather coat is a fairly good insulator. The difference between ambient temperature and feather coat temperature of these regions is largest at colder ambient temperatures, meaning that the feather coat is a more effective insulator at higher temperatures. The beak follows a similar pattern, but as ambient temperature increases, the variance greatly decreases (Fig. 5d). At the highest ambient temperature point, the beak temperature converges (i.e. low variance) and is above ambient temperature, indicating that the beak is being used as a radiator at high ambient temperatures (Greenberg et al. 2012). The eye follows a very different pattern with a nearly horizontal slope (Fig. 5e), so eye temperature is not correlated well with ambient temperature. As an uninsulated area, this is expected, though it is still significant that eye temperature at all ambient temperatures is lower than body temperature, suggesting that the birds have some mechanism other than insulation to avoid heat loss through the eye, perhaps blood flow control.

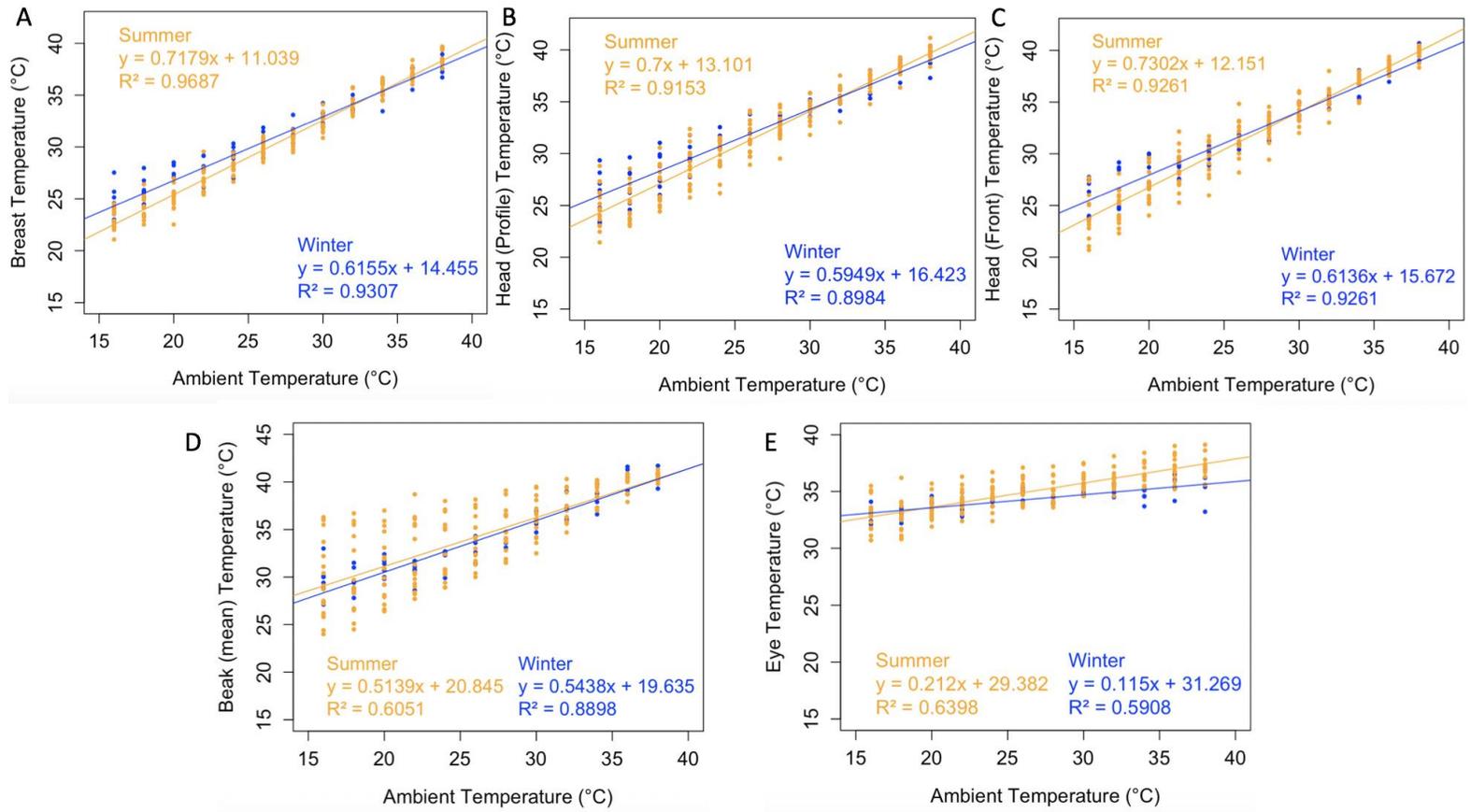


Figure 5: Thermal measurements of live birds at a) the breast, b) the head in profile, c) the head in a front view, d) the beak, and e) the eye. Each point represents thermal measures of one bird at a single ambient temperature. Individual birds are represented multiple times on each graph, but only once at each ambient temperature.

Thermal Measurements of the Feather Coat:

We calculated thermal performance by subtracting the temperature at the surface of the flat-skin from the temperature to which the flat-skin is exposed from underneath, which mimics internal body temperature. Thus, high values of thermal performance indicate a high level of heat retention by the feather coat. When the data are binned in the analysis as summer versus winter, the thermal performance of summer feather coats was statistically significantly, but only slightly (1°C) higher than the thermal performance of winter feather coats (Fig. 6a). However, this

statistical effect disappeared when we ran the analysis to relate thermal performance to date instead of season (Fig. 6b). Thus, date (seasonality) has no relationship with the thermal performance of flat-skins.

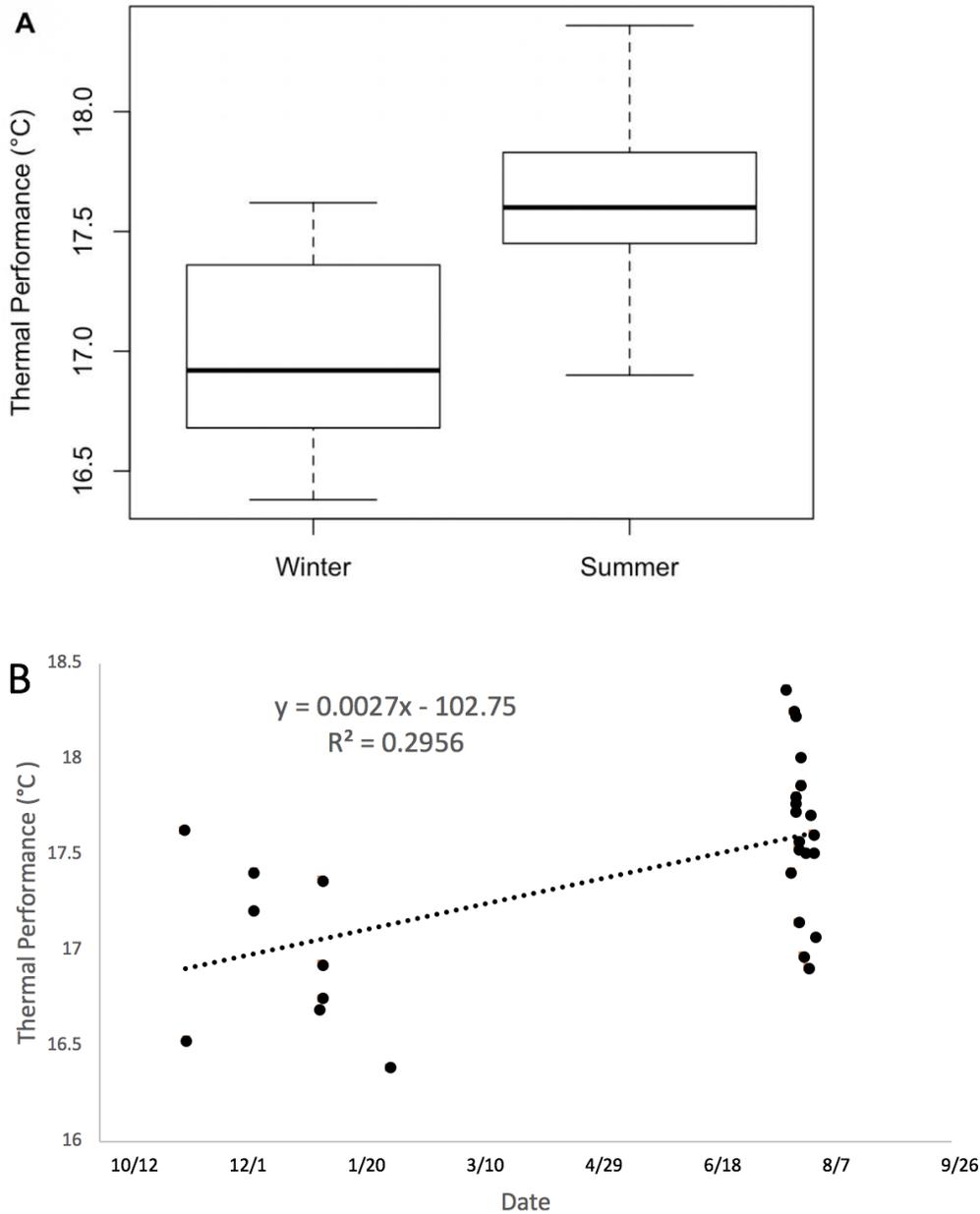


Figure 6: The thermal performance (temperature below the flat-skin - temperature at the surface of the flat-skin) values of feather coats a) in summer versus winter and b) according to date. Significance disappears when thermal performance is analyzed as a function of date.

Since in our study date is a proxy for expected feather condition, we examined the thermal performance against the ratio of broken barbs of all kind (pennaceous and plumulaceous) to the total number of barbs (Fig. 7). Feather wear did not explain the variation in thermal performance ($R^2 = .0391$), and the amount of variation in thermal performance is consistent among different amounts of feather wear. Thus, the amount of feather wear is not related to thermal performance.

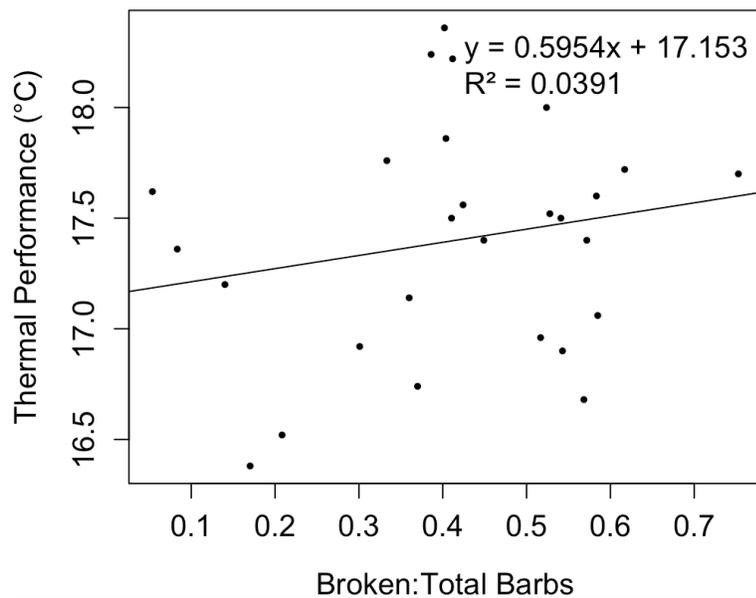


Figure 7: The thermal performance (temperature below the flat-skin - temperature at the surface of the flat-skin) values of feather coats a) in summer versus winter and b) according to feather wear. Feather wear does not predict thermal performance.

Comparison of Live Birds to Flat-skins:

In order to compare the thermal performance of feather coats on live birds to that of flat-skins, we subtracted the temperature at the surface of flat-skins from the temperature at the surface of the breast of live birds at an ambient temperature of 22°C, the ambient temperature at which flat-skins were measured in the laboratory. Thus, positive values mean that live birds lose more heat than flat-skins at the same ambient temperature. We did not find significant

differences in the comparison of live birds to flat-skins as a function of date (Fig 8, $R^2 = .0833$). However, in all cases, the temperature at the surface of the feather coat of live birds was greater than that of flat-skins (all values were positive), meaning that live birds had were releasing more heat to the environment than flat-skins alone. Although all live birds lost more heat at 22°C ambient temperature than their respective flat-skin, the variation in this difference was great, ranging from 1.677°C to 5.932°C.

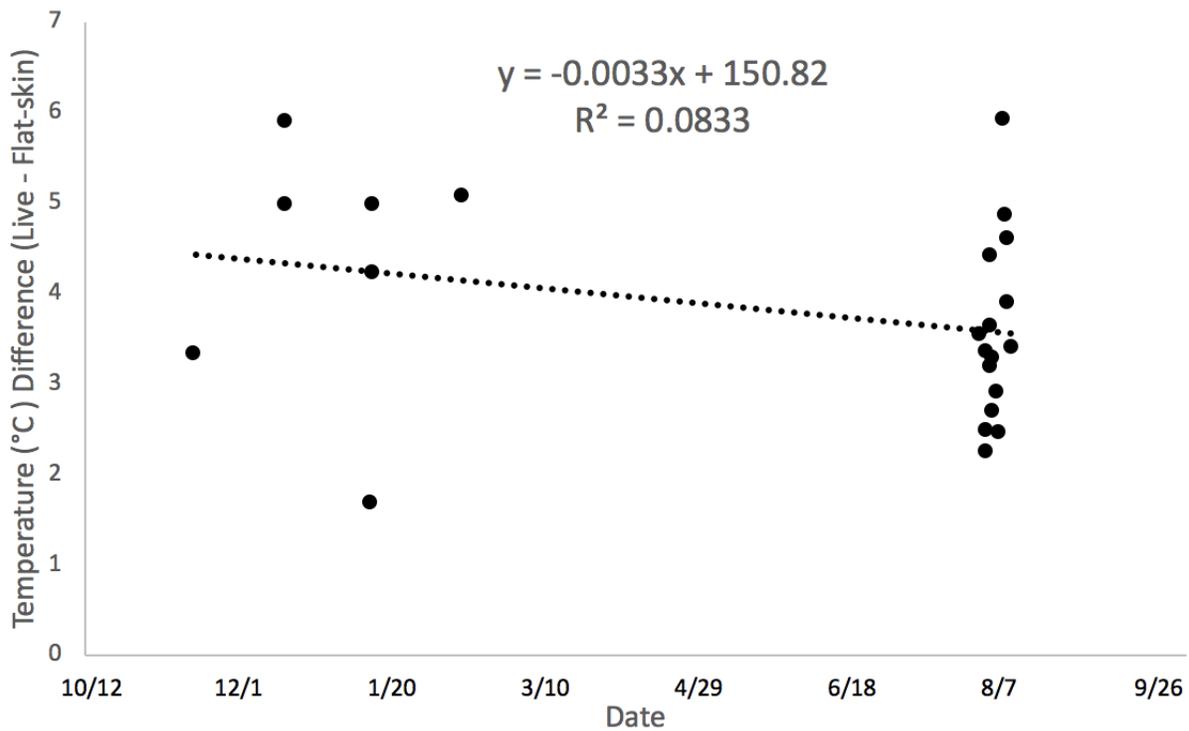


Figure 8: The difference between the temperature at the surface of the feather coat in flat-skins and live birds at 22°C in relation to collection date. Date explained very little variation in these differences.

We also examined the difference between the temperature at the surface of the feather coat in live birds and flat-skins against the ratio of broken barbs of all kind (pennaceous and plumulaceous) to the total number of barbs because our study uses date as a proxy for amount of feather wear (Fig. 9). We found that wear explained very little of the variation in the difference

between the temperature at the surface of the feather coat in flat-skins and live birds ($R^2 = .0373$).

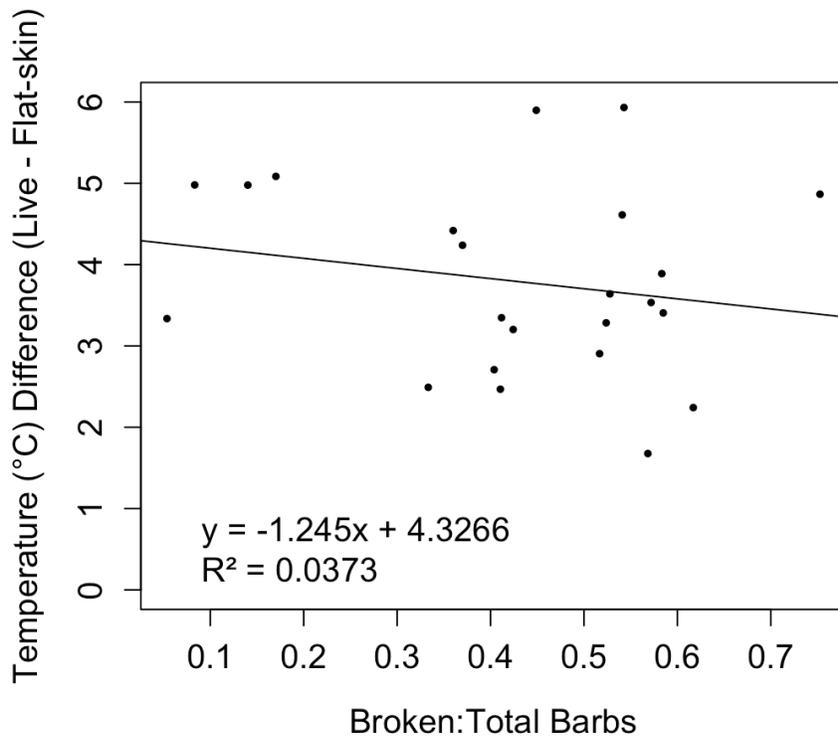


Figure 9: The difference between the temperature at the surface of the feather coat in flat-skins and live birds in relation to feather wear. Wear explained very little variation in these differences.

Discussion

Although a few other studies have quantified thermal performance, such as conductance values of feather coats (Taylor 1986, Novoa et al. 1994, Ward et al. 2001 and 2007), this is the first study to our knowledge which directly compares living birds, adjusting their thermal state to a range of temperatures, to their own feather coats in order to isolate the effect of the feather coat alone.

We found that feather wear did indeed increase from just after molt, over the winter months, to summer. Several other authors have reported this same result in other temperate

species (Wetmore 1921, Burt 1986, Willoughby 1986). Despite this feather wear, to our surprise and contrary to our initial hypotheses, we did not find significant differences between seasons in the thermal performance of either live birds or flat-skins.

The lack of thermal performance differences in live birds between seasons is particularly significant at temperatures above the upper critical temperature and below the lower critical temperature. If feather wear caused an increase in passive heat loss in worn summer feathers, then we might expect this effect to be the most pronounced at cold temperatures below the lower critical temperature, causing summer birds with worn feathers to lose more heat. Similarly, winter birds with non-worn feathers might have been expected to be less able to passively offload heat at hot temperatures above the upper critical temperature through unworn feathers. The evidence we present here showing that temperature at the surface of the feather coat in live birds did not differ between seasons and differed little from the ambient temperature, at any ambient temperature, suggests strongly that house sparrows are tightly guarding their interior temperatures. It appears that we were simply measuring the ambient temperature effect on the surface feathers.

Most surprisingly, we found that flat-skins had higher thermal performances at 22°C than the live birds they were taken from. This result contradicts our original hypothesis that live birds would exhibit higher thermal performances than flat-skins, because live birds have several thermoregulatory mechanisms, in addition to the feather coat, available to them (e.g. fat storage, behavioral thermoregulation, and physiological acclimation). This peculiar result may be an artifact of captivity stress during experiments, thus raising the temperature at the surface of the feather coat through an additional increment of heat loss, but this is merely speculative.

Regardless of the reasoning, the result that flat-skins had a higher thermal performance than live birds suggests that the feather coat alone provides a significant amount of insulation.

Even though, as expected, feather wear varied significantly with season, with summer birds exhibiting much more wear overall, we found no evidence that feather wear reduced or changed the thermal performance of flat-skins. Although we did not quantify feather number, feather number has long been known to vary between seasons in temperate zone birds (Wetmore 1936) as well as in house sparrows specifically (Staebler 1941, Barnett 1970), with more feathers in the winter than in the summer. Thus, we would expect feather number to function similarly to feather wear, with a lower feather number in the summer reducing thermal performance. However, our measurements of feather coats integrate all components of the feather coat; thus, the effect of feather number is included in our measurements of thermal performance. Therefore, considering that we did not find differences in thermal performance with these integrative measures, it is likely that the seasonal loss of whole feathers does not pose a significant enough cost to reduce thermal performance.

Our study species, house sparrows, are extremely successful at invading new areas over a wide array of thermal and climatic conditions. Perhaps this species is particularly good at avoiding heat loss through the feather coat. Species that exhibit less adaptability and are more geographically and thermally confined may show seasonal differences in thermal performance, but this remains to be explored. Additional studies using our flat-skin measurement methods on species with limited thermal ranges could address this question. Moreover, species such as the American goldfinch, which molt twice during the year and show differences in feather type composition between molts (Middleton 1986), may show differences in thermal performance between seasons, but these differences would be due to feather morphology, not feather wear.

There is still a significant gap in the understanding of how feather morphology affects heat loss. We are not aware of any studies which have quantified how variation in different aspects of feather morphology, such as feather type, plumulaceous versus pennaceous barbs, amount of down, etc., affect heat loss.



Figure 10: A worn contour feather.

Taken together, our results suggest strongly that feather wear is not biologically significant to heat loss, even at the level of wear we documented (Fig. 10), and that house sparrows molt before feather wear becomes significant enough to affect heat loss. However, feathers serve many functions, and it is possible that other aspects of the functional capacity of the feathers, such as water-repellency, are affected by wear, and may drive molt before the thermal performance of the feather coat is much affected. Additionally, considering that pennaceous wear was much more extensive than plumulaceous wear, it is possible that plumulaceous barbs are more important to insulation than pennaceous barbs. This would align with previous ideas of feather functional morphology (Lucas and Stettenheim 1992), but quantitative research is necessary to understand this fully. Feather wear through the course of

the year has long been known (Wetmore 1921, Burt 1986, Willoughby 1986); this study illustrates the importance of directly measuring its effect.

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