

## DOES WHITE TAIL PATCH SIZE INDICATE QUALITY IN MALE CERULEAN WARBLERS (*SETOPHAGA CERULEA*)?

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**ABSTRACT.**—Within species of birds, variation in plumage may allow potential mates or competitive rivals to quickly assess the quality of an individual. Little is known about the role of white tail feather patches (“tail white”) in male Cerulean Warblers (*Setophaga cerulea*) and whether variation in patch size could serve as a signal. We hypothesized that the size of tail white patches in males acts as an honest signal of quality, with larger white patches indicating high quality males. We measured and compared the area of tail white to four estimates of quality (age, structural size, body mass, and blood parasite load) in 71 male Cerulean Warblers at the Queen’s University Biological Station in eastern Ontario. We found that males 2 years old or older had significantly larger tail white patches than 1 year old males, and that structurally larger males (estimated by wing length) had significantly larger tail white patches than smaller males. Our best-performing statistical model suggested that heavier individuals had larger areas of tail white, but this relationship depended on wing length: white positively covaried with body mass in smaller individuals (shorter wings), but not in larger individuals. Our findings suggest that size of tail white patches may provide information on some, but not all, aspects of quality of male Cerulean Warblers; however, we do not know if this information is perceived and used by other Cerulean Warblers in nature. Received 6 October 2014. Accepted 17 September 2015.

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Intraspecific variation in plumage is widespread in birds. Variability in plumage can be important for intraspecific communication, where plumage may function as a signal of individual identity, reproductive strategy, kinship, or individual quality (Burley and Bartels 1990, Sætre and Slagsvold 1992, Dale et al. 2001, Dale 2006). In particular, plumage that functions as a signal of quality can allow potential mates or competitive rivals to quickly assess the age, size, or condition of an individual (Rohwer 1975, Kodric-Brown and Brown 1984). Sexual selection often favors quality-dependent signal expression, which maintains signal honesty (Zahavi 1975, Kodric-Brown and Brown 1984, Nur and Hasson 1984, McGlothlin et al. 2005). More elaborate plumage traits are often more costly to produce, display, or maintain, and thus only individuals of good quality (older, larger, or healthier) can afford such costs (Zahavi 1975, Kodric-Brown and Brown 1984). Consequently, intraspecific variation in honest signals is usually related to age, aspects of the environment

that influence social status or health, genetic quality, or an interaction between factors (Rohwer 1975, Hamilton and Zuk 1982, Kodric-Brown and Brown 1984, Hill 2000, McGraw et al. 2003).

In particular, honest signals related to social status may reflect aspects of individual quality such as age or structural body size (e.g., Veiga 1993, McGlothlin et al. 2005). Age can be related to individual quality in a social context, because younger birds are often less experienced in aggressive conspecific interactions and socially inferior to older birds (Ketterson 1979, Rohwer et al. 1981, Sandell and Smith 1991). Similar to age, structural body size can be related to individual quality because larger birds are usually dominant to smaller birds, and thus have primary access to resources (Fretwell 1969, Balph et al. 1979, Ketterson 1979). The honesty of signals that advertise age or structural size can be socially enforced. Males whose level of character expression does not correspond to their dominance or competitive abilities may be prosecuted in male-male competitions in cases where trait expression exceeds their abilities, or suffer from decreased mating success when trait expression falls below their abilities (Rohwer 1977, McGlothlin et al. 2005). For example, structurally large male Dark-eyed Juncos (*Junco hyemalis*) with large patches of white in their tail feathers have higher mating and competitive success than smaller males

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displaying large white patches (McGlothlin et al. 2005). Males with white patches that are too large for their size might be more likely to be attacked by other males, thus keeping the signal honest (McGlothlin et al. 2005).

Honest signals can also provide information about an individual's health, such as body mass or parasite load. Theory suggests that energy and resources are first allocated towards maintenance and health and only afterwards to the production or maintenance of secondary sexual traits (Kodric-Brown and Brown 1984). Conspecifics may infer that an individual is of good quality (e.g., healthy body mass) if this individual can expend resources on producing or maintaining a non-essential ornament (Kodric-Brown and Brown 1984). Expression of sexual ornaments can also indicate resistance to current parasites or disease, as well as the ability to pass on resistant genes to future offspring, when the expression of the ornament relies on good health (Hamilton and Zuk 1982). Furthermore, because many birds only replace their feathers at discrete time periods (molt), plumage ornaments have the potential to reflect an individual's health at the time of feather development. Molting is an expensive process that requires high levels of energy and nutrient allocation in birds (Murphy and King 1992, Murphy 1996), and thus an individual's health and ability to acquire resources during molt may influence the expression of an ornament (Hill and Montgomerie 1994, Hill 2000, McGlothlin et al. 2007). Because of the fact that many birds fully replace their feathers only once a year, plumage ornaments can be useful signals of short or long-term health, depending on the time since molt (Hill et al. 1999).

Cerulean Warblers (*Setophaga cerulea*) have white patches on their tail feathers ("tail white"; Hill et al. 1999) that vary in size among individuals and tend to be more pronounced in males (Pyle 1997). Males have been observed flashing their tail feathers during aggressive territorial displays (EFP and PRM, pers. obs.), and may use similar displays in courtship. In fact, previous work has shown that the size of white tail patches in male Cerulean Warblers provides information about condition during the previous breeding season (Boves et al. 2014). Furthermore, several studies have demonstrated that large, white tail and wing feather patches are costly to produce, maintain, or display in other species (e.g., Kose and Møller 1999; Török et al. 2003;

McGlothlin et al. 2005, 2007; Griggio et al. 2011). These observations suggest that tail white may be acting as an honest signal of male quality in Cerulean Warblers, as they do in Dark-eyed Juncos. Here, we test a central prediction of the hypothesis that the size of tail white patches in male Cerulean Warblers is an honest signal of male quality, with larger white patches signaling males of higher quality (age, structural size, or health). If this hypothesis is true, then we predicted that (1) older males (older than 1 year) will have more tail white than younger males (1 year old), (2) structurally larger males (estimated by wing length and tarsus length) will have more tail white than smaller males, and (3) healthier males (estimated by body mass and blood parasite load) will have more tail white than unhealthy males.

## METHODS

### Field Capture and Measurements

We sampled 71 male Cerulean Warblers from the Queen's University Biological Station (44° 34' N, 76° 19' W) near Elgin, Ontario, Canada from May–July 2010. We caught males in mist-nets using targeted playback paired with presentation of a male model of a Cerulean Warbler. After capture, we banded each individual with a numbered aluminum band from the Canadian Wildlife Service and gave each warbler a unique combination of colored bands. We aged each male based on plumage coloring and feather wear, where 1 year old males ("second-year" or SY) have worn primaries and tail feathers, show differential wear and pattern of wing coverts, and exhibit greener plumage than males that are 2 years old or older ("after-second-year males" or ASY; Pyle 1997).

For each captured male, we measured its unflattened wing chord (mm) using a wing ruler, tarsus length (mm) using a caliper, and mass (g) using a Pesola spring scale. We checked the accuracy of our Pesola scale using standard weights before and after the field season. Prior to each measurement, we checked that the Pesola scale read zero, and adjusted the scale to zero if needed. Our measurements of mass were accurate to  $\pm 0.2$  g. All field measures were made by MAC to control for inter-individual variation in measurement. In order to quantify the area of tail white for each male, we photographed six individual feathers from each bird's tail from

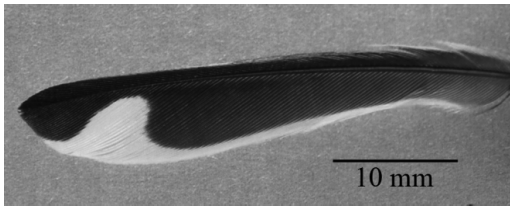


FIG. 1. A photograph of an inner left rectrix (R3) on a male Cerulean Warbler (*Setophaga cerulea*), aged 2 years old or older, against a green paper background with a linear scale of 10 mm.

a dorsal view. Each tail is made up of six pairs of feathers (“rectrices”). We photographed the left six rectrices of the tail because they were easiest to manipulate and photograph in the hand. If a bird was missing a feather from their left side, then we photographed the right side instead. We photographed each left feather separately in the shade using a Nikon D50 camera (Nikon Canada Inc., Mississauga, Canada). Each feather was photographed against a green paper background with a visibly marked scale of 10 mm (Fig. 1).

We also obtained a small blood sample from each individual for parasite analysis by pricking the brachial vein with a sterile 23.5 gauge needle. We then collected between 15–20  $\mu$ L of blood from each male using a heparinized microcapillary tube. Using this blood sample, we made a blood smear on a clean glass microscope slide. We used a Camco Stain Pak (model 702; Cambridge Diagnostic Products Inc., Fort Lauderdale, FL, USA) that involves a three-step process to fix and stain each blood smear. We saved the remainder of the blood sample for future genetic work.

#### Tail White Measurements

We calculated the total area of white in all six left rectrices as a proxy of tail white for each male. In order to determine the area of white in each feather, we used the program ImageJ to analyze the photos (Rasband 2011). We loaded each photo of interest into ImageJ and set the scale (pixels/mm) for the image using the 10 mm scale line in the photo and the “set scale” function in the program. After setting the scale, we manually set an appropriate threshold value in order to segment the white tail patch from its background. After the image threshold was set, we used the “wand tool” in ImageJ to trace the white patch, including the trailing white edge, and then used the program to calculate the area of the traced white patch in  $\text{mm}^2$ .

We completed these steps for all six rectrix photos for each individual. We summed the six white patch areas to obtain an estimate of the overall area of tail white for the individual. All tail white measures were made by EFP.

The left and right rectrices are not exactly symmetrical within individuals (i.e., may differ in their area of tail white), and thus there is potential error involved when using the left side as a proxy for total area of white in the tail. In order to determine if the area of white in the left rectrices provides an accurate index of overall tail white, we photographed the left and right rectrices of six Cerulean Warbler specimens from the Royal Ontario Museum. We followed the same tail white quantification methods outlined above. We performed a Pearson’s product-moment correlation between the area of tail white in the left rectrices and the area of tail white in the right rectrices to determine whether the area of white on the left rectrices predicted the area of white on the right rectrices, and thus provided an accurate index of the overall area of white on the tails of male Cerulean Warblers.

Additionally, it is possible that the size of a white tail patch is simply proportional to the size of the rectrix, where structurally larger individuals (estimated by tarsus and wing length) also have larger rectrices. We could not accurately measure the size of rectrices in the field, and thus could not control for rectrix size in our analyses. Instead, we tested whether structurally larger males (estimated by tarsus and wing length) had a larger proportion of white in the part of the tail that is publicly displayed compared to smaller males, and whether this relationship was consistent with the relationship between the area of tail white ( $\text{mm}^2$ ) and structural size. We tested this using a non-random subsample of 24 males from our dataset that exhibited small to large areas of tail white in their left rectrices. We selected these 24 individuals by ordering all individuals from our full sample of 71 males from smallest to largest areas of tail white in a spreadsheet and then sampling every third individual starting from the individual with the smallest area of tail white. For each sample individual, we measured the proportion of white area on each left rectrix within an area defined by a standard length of tail feather (20 mm), measured from the posterior tip of the feather and up the feather vein. We chose to use a standard length of 20 mm because this measure was long enough to include the large white patch in all feathers

(but not the trailing white edge). We used the same photographs and tail white quantification methods in ImageJ as outlined above to calculate both the area of white and the area of black on each 20 mm segment of feather, and then calculated the proportion of white in each feather as: (area of white)/(area of white + area of black). We summed the proportion of white in each feather across all six left feathers to come up with a total proportion of tail white for subsequent analysis.

#### Parasitemia Measurements

We created a saturation curve for five randomly selected slides to determine the number of red blood cells (RBCs) needed to attain a consistent measure of parasitemia for an individual. We analyzed each of the five chosen slides using a Leica DM LS microscope (Leica Microsystems Inc., Concord, Canada) at 1,000-times magnification under oil immersion. We began counting RBCs in an arbitrary position in the periphery of the blood smear. We continued counting the number of parasitized RBCs per total number of RBCs in sequential fields of view until the total proportion was unchanged and the curve became saturated (i.e., level). After averaging the point of saturation between these five slides, we added an additional 500 RBCs to increase confidence. Based on this initial work, we defined parasitemia as the number of parasitized RBCs per 3,000 RBCs. All parasitemia measures were made by EFP.

In order to determine parasitemia for each individual, we used a Leica DM LS microscope at 1,000-times magnification under oil immersion. We began by scanning each slide for 20 mins to determine the prevalence of *Haemoproteus* and *Plasmodium* (Godfrey et al. 1990). If we did not detect any parasitized RBCs of either parasite genera within 20 mins, we deemed the individual uninfected. If we only detected one parasite genus before 20 mins was finished, we continued scanning for the second genus for the remainder of the 20 mins. To determine parasitemia of each individual, as with establishing our protocol, we began counting RBCs in an arbitrary location in the periphery of the blood smear. We counted the number of parasitized RBCs per total number of RBCs in a tally, counting RBCs in successive fields of view until we reached a total number of 3,000 RBCs. To calculate parasitemia for each slide, we divided the total number of parasitized RBCs by 3,000 RBCs for each parasite genus separately. To assess the repeatability of our

parasitemia measurements, we re-counted parasitemia for 15 individuals. We selected 5 unparasitized individuals and 10 parasitized individuals varying in parasitemia infection level. We performed an intraclass correlation between the original parasitemia and the re-counted parasitemia to determine repeatability.

#### Statistical Analyses

We used R (R Core Team 2013) to perform all statistical analyses. In our analyses, we only included individuals for which we had tail white, mass, tarsus and wing length, and parasitemia measurements ( $n = 71$ ).

*Age and Tail White.*—To test our first prediction that older males have a larger area of tail white than younger males, we used a two sample *t*-test, with the area of tail white as the response variable, and age class (SY or ASY) as the predictor variable. We first tested if the sample variances differed between the two age classes using Fisher's *F*-test. Sample variances did not differ ( $F = 0.92$ ,  $df = 55, 14$ ,  $P = 0.77$ ), so we proceeded with a Student's two sample *t*-test.

*Structural Size and Tail White.*—To test our second prediction that structurally larger males have more tail white than smaller males, we used two measures of structural size: tarsus length and wing length. Tarsus length and wing length were not significantly correlated with each other (Pearson's correlation,  $t = 1.4$ ,  $df = 69$ ,  $P = 0.16$ ,  $r = 0.17$ ). We tested the prediction that tail white increases with tarsus and wing length using a generalized linear model with the area of tail white as the response variable, and age class, tarsus length, and wing length as predictor variables. We also included all possible two-way interactions between predictor variables in the model. We initially included second order polynomial terms for tarsus and wing length in the generalized linear model to address possible non-linear relationships between tail white and tarsus or wing length; however, upon inspection, the model with polynomial terms yielded similar results to the model without, so we excluded the polynomial terms from the model for simplification. We validated the model by comparing residuals versus fitted values to verify homogeneity, testing if residuals deviated from normality using a histogram and Shapiro-Wilk test, and examining residuals versus tarsus and wing length to check independence. We further tested for homogeneity of variances of residuals for age classes using a Bartlett's test.

The model fit the data well. In addition, all Cook's Distance values were  $<0.5$ , suggesting that no single data point had large influences on the model (Zuur et al. 2009). After validating the model, we used the dredge function in the MuMIn statistical package in R (Bartoń 2014) to compare among models with all possible combinations of predictor terms. We identified the best-performing model as the model with the lowest Akaike's Information Criterion score, adjusted for small sample sizes (AICc). We validated the best-performing model in the same way that we validated the global model above. We report the results of our best-performing model.

*Health and Tail White.*—To test our third prediction that healthier males have more tail white than less healthy males, we used two measures of relative health: body mass and parasite load. In all analyses, we treated health (or condition) as the dependent variable, because tail white is determined in late summer to early fall, and the health of the birds in the subsequent breeding season cannot directly influence the tail white that we measured. Thus, we asked if tail white (grown in late summer, early fall) predicted our estimates of health during the subsequent breeding season. Body mass and parasite load were not significantly correlated with each other (Spearman's rank correlation,  $S = 55839$ ,  $P = 0.60$ ,  $\rho = 0.06$ ), consistent with earlier work that found no relationship between size-corrected body mass and *Haemoproteus* parasite load in Cerulean Warblers (Gibb et al. 2005).

We tested the prediction that body mass increases with tail white using a generalized linear model with body mass as the response variable, and the area of tail white, age class, date of capture (to control for differences in body mass based on when individuals were caught), and tarsus and wing length (to control for structural size) as predictor variables. We also included all possible two-way interactions between predictor variables in the model. We validated the model following the same methods as described above for our second prediction. However, the model for body mass suffered from heterogeneity of variances; residual variance differed significantly between age classes (Bartlett test,  $K^2 = 7.60$ ,  $df = 1$ ,  $P = 0.006$ ). To address this issue, we ran a generalized least squares model, specifying different variances for each age class using the varIdent function in the nlme statistical package in R (Pinheiro et al. 2009), following Zuur et al. (2009). The generalized

least squares model specifying different variances was a significant improvement over a generalized least squares model that did not specify different variance structures (ANOVA,  $P = 0.028$ ,  $\Delta AIC = 2.85$ ). Validation of the generalized least squares model suggested a good fit to the data. We then compared model performance for all possible combinations of predictor terms and validated the best-performing model following the same methods as described above for our second prediction. We report the results of our best-performing model.

We tested the prediction that parasite load is related negatively to tail white using a zero-inflated Poisson model in the R package pscl (Jackman 2010) with parasite load (summed number of observed parasites of both genera over 3,000 RBCs) as the response variable, and the area of tail white and age class as factors within a saturated model (following methods outlined in Zuur et al. 2009). We used a zero-inflated model because we found no parasites in many of our samples. Upon model validation, our model showed evidence of overdispersion, so we instead used a zero-inflated negative binomial model. We used the lrtest function in the package lmerTest (Zeileis and Hothorn 2002) to test for improvement between the Poisson and negative binomial distribution models, and found the latter to be a significant improvement ( $X^2 = 373$ ,  $df = 6$ ,  $1$ ,  $P < 0.001$ ). We then compared model performance for all possible combinations of predictor terms and validated the best-performing model following the same methods that we used in our second prediction. We also ran one additional test to examine if parasitized birds had less tail white than unparasitized birds. To test this hypothesis, we ran a generalized linear model with the area of tail white as the response variable, and parasitized (yes or no) and age class as predictors in a saturated model. We validated the model, compared model performance for all possible combinations of predictor terms, and validated the best-performing model following the same methods as described above for our second prediction. We report the results of our best-performing model for both parasitemia tests.

*Proportion versus Area of Tail White.*—Using our subsample of 24 males, we tested whether structurally larger males (estimated by tarsus and wing length) had a larger summed proportion of white in the outer 20 mm of their tail feathers compared to smaller males, and whether this

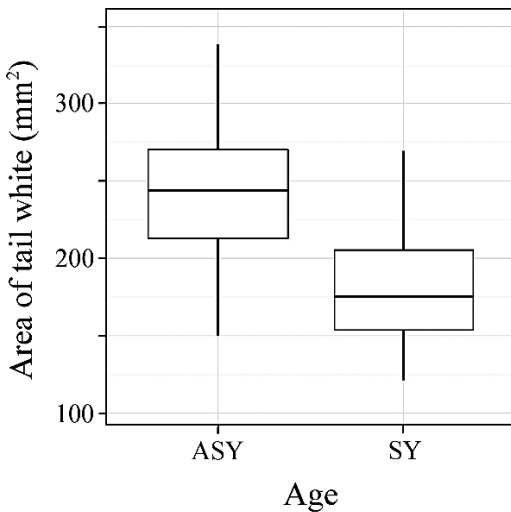


FIG. 2. A comparison of the area of tail white between age classes in male Cerulean Warblers (*Setophaga cerulea*). On average, ASY males (2 years old or older) have significantly more tail white than SY males (1 year old; Student's *t*-test,  $t = 4.52$ ,  $df = 69$ ,  $P < 0.001$ ). The mid lines in the box plots display the 50<sup>th</sup> percentile; the boxes enclose the 25<sup>th</sup>–75<sup>th</sup> percentiles; each whisker extends an additional 1.5  $\times$  interquartile range of the data from the box.

relationship was similar to the relationship between the area of tail white ( $\text{mm}^2$ ) and structural size. We used a generalized linear model with the summed proportion of white in the outer 20 mm of the left rectrices as the response variable, and age class, wing length, and tarsus length as predictor variables. We included all possible two-way interactions between predictor variables in the model. We used a separate generalized linear model to test whether structurally larger males had a larger area of tail white than smaller males within our subsample of 24 males (similar to our second prediction above). We included the area of tail white as the response variable, and the same predictor variables as above in the model. We validated both models, compared model performance for all possible combinations of predictor terms, and validated the best-performing models following the same methods as described above for our second prediction.

## RESULTS

Male Cerulean Warblers were highly variable in the area of white in their tails, with some males showing more than double the area of white

compared with other males (Fig. 2). Based on our data from the specimens of Cerulean Warblers at the Royal Ontario Museum, we found that the area of white in the left rectrices covaried positively with the area of white in the right rectrices (Pearson's product-moment correlation,  $t = 58.90$ ,  $df = 4$ ,  $P < 0.001$ ,  $r = 0.999$ , slope = 1.05). The high value of  $r$  suggests that the area of tail white on one side of the tail accurately reflects the area of white across the entire tail.

### Age and Tail White

ASY male Cerulean Warblers had significantly larger areas of white in their left rectrices than SY males (Student's *t*-test,  $t = 4.52$ ,  $df = 69$ ,  $P < 0.001$ ; Fig. 2).

### Structural Size and Tail White

We found that the best-performing model contained only age and wing length, with wing length correlated positively with the area of tail white in male Cerulean Warblers, independent of age (Generalized Linear Model, slope = 8.05, SE = 3.99,  $t = 2.01$ ,  $n = 71$ ,  $P = 0.048$ ; Fig. 3). We report all models with a  $\Delta \text{AICc}$  value  $< 2$  in Appendix 1.

### Health and Tail White

When we used body mass as a proxy of health, we found that the best-performing model contained the area of tail white and the interaction between tail white and wing length, as well as other variables (age, wing length, tarsus length, age by tarsus length, and age by wing length interactions), as predictors of body mass. We report all models with a  $\Delta \text{AICc}$  value  $< 2$  in Appendix 2. Although these predictor variables were retained in the best-performing model, they were not statistically significant (i.e.,  $P < 0.05$ ). Individuals with larger areas of tail white had higher body mass (Generalized Linear Model, slope = 0.093, SE = 0.048,  $t = 1.92$ ,  $n = 71$ ,  $P = 0.060$ ), with the effect of tail white depending on wing length: white covaried positively with body mass in smaller individuals (shorter wing length), but not in larger individuals (Generalized Linear Model, interaction effect = -0.0013, SE = 0.00072,  $t = -1.86$ ,  $n = 71$ ,  $P = 0.068$ ; Fig. 4).

We did not find evidence that the area of tail white predicts parasite load; the best-performing model was the null model. Additionally, we found no significant difference in the area of tail white between parasitized and unparasitized males; the

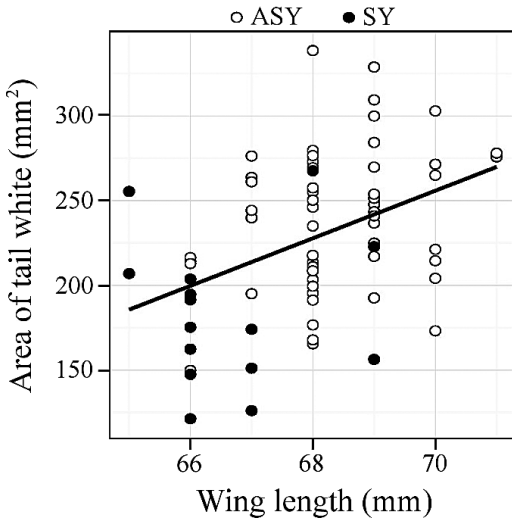


FIG. 3. Scatter plot of the area of tail white (mm<sup>2</sup>) and wing length (mm) in male Cerulean Warblers (*Setophaga cerulea*). Males with longer wings exhibit larger patches of tail white, independent of age (Generalized Linear Model, slope = 8.05, SE = 3.99,  $t = 2.01$ ,  $n = 71$ ,  $P = 0.048$ ). Data for ASY males (2 years old or older) are represented by open circles, and data for SY males (1 year old) are represented by closed circles. We excluded age class from the model shown (black line) to simplify the presentation of results; the intercepts for age class were significantly different, but the interaction term between age class and wing length was not.

best-performing model contained age as the only predictor of tail white. We found that our parasitemia measurements for an individual were repeatable but that the intraclass correlation was not high (Intraclass Correlation, ICC = 0.54,  $F = 3.30$ ,  $df = 14$ ,  $P = 0.014$ ).

Proportion versus Area of Tail White

Based on our subsample of 24 males, the relationship between the proportion of tail white on the outer 20 mm of rectrices and structural size was similar to the relationship between the area of tail white and structural size (Fig. 5); in both cases, the best-performing model contained wing length as the only predictor of tail white. Males with longer wings had larger areas of tail white (Generalized Linear Model, slope = 0.096, SE = 0.040,  $t = 2.38$ ,  $n = 24$ ,  $P = 0.027$ ), and also had larger summed proportions of tail white in the outer 20 mm of their six left rectrices (Generalized Linear Model, slope = 12.90, SE = 5.28,  $t = 2.44$ ,  $n = 24$ ,  $P = 0.023$ ).

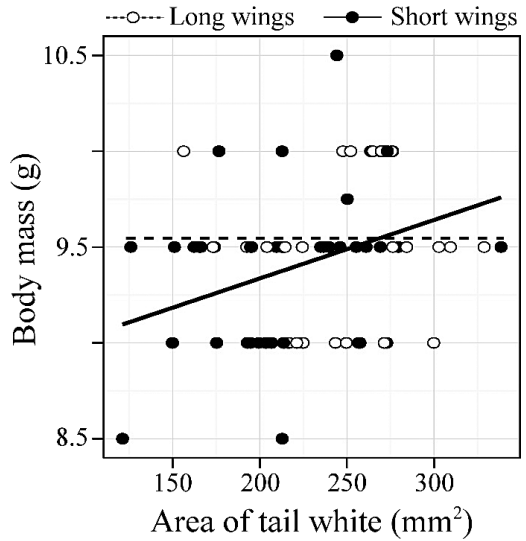


FIG. 4. Scatter plot of body mass (g) and the area of tail white (mm<sup>2</sup>) in male Cerulean Warblers (*Setophaga cerulea*). Although not statistically significant, both tail white and the interaction between tail white and wing length were retained as predictors in our best-performing statistical model (lowest AIC<sub>c</sub>) explaining variation in body mass. Individuals with larger areas of tail white had higher body mass (Generalized Linear Model, slope = 0.093, SE = 0.048,  $t = 1.92$ ,  $n = 71$ ,  $P = 0.060$ ), where the effect of tail white depended on wing length: white covaried positively with body mass in smaller individuals (shorter wing length), but not in larger individuals (Generalized Linear Model, interaction effect = -0.0013, SE = 0.00072,  $t = -1.86$ ,  $n = 71$ ,  $P = 0.068$ ). Data for smaller males (shorter wings) are represented by closed circles and a solid trend line. Data for larger males (longer wings) are represented by open circles and a hatched trend line. Wing size groups are split by the midpoint value of wing length for the dataset (small = 65–68 mm; large = 69–71 mm).

DISCUSSION

The area of white in the tails of male Cerulean Warblers varied with their age and structural size, and possibly also their body mass. We found that older males (>1 year old) exhibit larger patches of tail white than younger males (1 year old; Fig. 2), and that structurally larger males (with longer wings) exhibit larger patches of tail white, both before and after controlling for the effects of age class (Fig. 3). The relationship between wing length and tail white was similar when we estimated tail white by the total area of white, or by the proportion of white in the outer 20 mm of their feathers (Fig. 5). We also found evidence that body mass varied with the area of tail white in

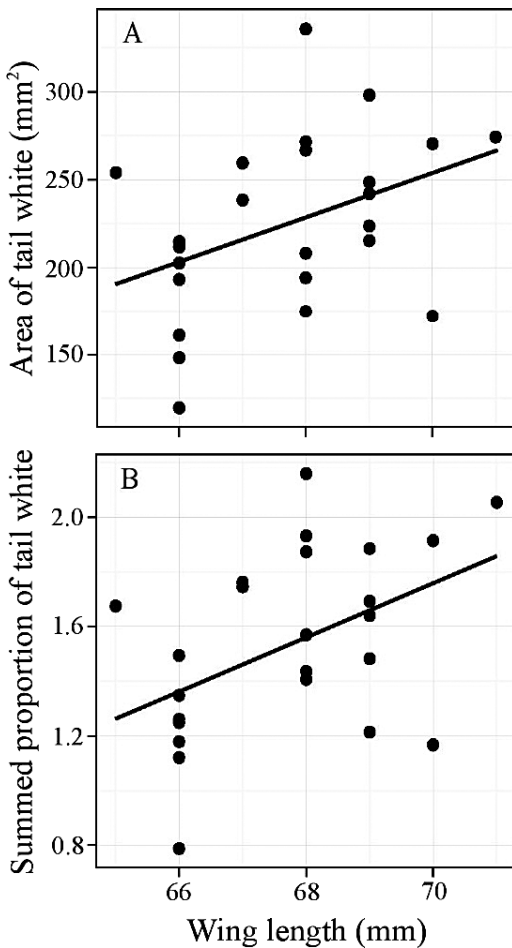


FIG. 5. Two representations of tail white by wing length for a subset of male Cerulean Warblers (*Setophaga cerulea*;  $n = 24$ ). Males with longer wings have larger areas of tail white on their six left rectrices (Generalized Linear Model, slope = 0.096, SE = 0.040,  $t = 2.38$ ,  $n = 24$ ,  $P = 0.027$ ; A). Males with longer wings also have larger summed proportions of tail white in the outer 20 mm of their six left rectrices (Generalized Linear Model, slope = 12.90, SE = 5.28,  $t = 2.44$ ,  $n = 24$ ,  $P = 0.023$ ; B).

smaller individuals (with shorter wings), but not in larger individuals (Fig. 4). In contrast, structural size estimated by tarsus length did not covary with tail white, and tail white was a poor predictor of male condition as measured by parasitemia. Taken together, our findings suggest that tail white in male Cerulean Warblers signals some, but not all, aspects of male quality, although we lack information on how this variation is perceived and used by other Cerulean Warblers in nature.

Older and structurally larger males might have larger tail white patches for several reasons. In general, older and larger males are dominant to younger and smaller males, and thus can occupy territories with better food availability (Holmes et al. 1996, Huhta et al. 1998, Keyser and Hill 2000). Older or larger males with better access to food during molt may gain more time and energy to organize feather keratin and surrounding melanin pigments (Mennill et al. 2003), allowing them to produce larger, more attractive white badges than their subordinate conspecifics. For example, male Dark-eyed Juncos with access to an enriched diet during feather development grew larger white tail patches than males that received a sustenance diet, and larger and more dominant Dark-eyed Juncos typically have more tail white than smaller males (McGlothlin et al. 2005, 2007). Furthermore, Boves et al. (2014) found that older ASY male Cerulean Warblers had significantly larger tail white patches and higher tail feather growth rates than younger SY males, suggesting that SY males may have experienced nutritional constraints during feather development. In our study, both ASY and SY male Cerulean Warblers would have grown their tail feathers during the previous breeding season, but in the case of younger SY Cerulean Warblers, tail feathers were mostly grown shortly after fledging when the warblers were inexperienced at foraging on their own (Boves et al. 2014). These observations suggest that older or larger (dominant) males might produce large white tail patches because they have better access to high quality food during feather development. Alternatively, young or small (subordinate) males may express less tail white because of stress-induced processes triggered by limited resources (McGlothlin et al. 2007).

Alternatively, younger SY males may have less tail white than older ASY males because of selective pressures that favor delayed plumage maturation. According to this hypothesis, younger males display duller, less elaborate plumage to signal their subordinate status in order to evade aggression from older birds (Rohwer et al. 1980, Lyon and Montgomerie 1986). If tail white is a trait assessed by potential female mates, then adult male Cerulean Warblers should target their aggression towards other males who display attractive ornaments, because they are more serious competitors. Thus, the younger males in our study may have expressed less tail white in order to signal their



subordinance and avoid the costs associated with physical confrontation. However, Boves et al. (2014) found that, even though SY male Cerulean Warblers had smaller tail white patches than ASY males on average, some SY males had larger white patches than ASY males, and SY males often made substantial efforts to secure mates and engage in aggressive male-male interactions. We also found overlap in the size of tail white patches between SY and ASY males (Fig. 2), and observed that SY males often responded aggressively to perceived territorial intruders (conspecific playback and model presentation). These findings suggest that delayed plumage maturation in SY male Cerulean Warblers may not be an adaptive life history strategy to limit conspecific aggression (Hawkins et al. 2012, Boves et al. 2014), or may be selectively used by SY males.

Structurally larger males may have more tail white because of correlational selection on structural size and tail white, where tail white honestly signals size. Correlational selection can occur when a sexual trait (e.g., tail white) and a trait that influences phenotypic quality (e.g., structural size) impact fitness in an interactive way (Lande and Arnold 1983, Sinervo and Svensson 2002, McGlothlin et al. 2005). For example, white tail patch size and structural size are under correlational selection in male Dark-eyed Juncos, where the fittest individuals are structurally large and display large tail white patches (McGlothlin et al. 2005). Under correlational selection, individuals with mismatched trait combinations (e.g., small males with large tail white patches or large males with small patches) would be selected against during intrasexual competition and/or mate choice (McGlothlin et al. 2005). Such correlational selection might have resulted in a genetic integration of tail white and structural size, which would maintain the honesty of tail white as a signal of quality (McGlothlin et al. 2005). Similar to juncos, large tail white patches in Cerulean Warblers might represent a sexual trait of high value, and large structural size (a possible proxy of dominance) might represent high phenotypic quality. Thus, our findings that larger male Cerulean Warblers displayed significantly larger tail white patches than smaller males suggests that correlational selection might act on these two traits.

Consistent with our third prediction, we found some evidence that heavier male Cerulean

Warblers had larger patches of tail white, but this relationship was present only in structurally smaller males (as estimated by wing length). This interaction between tail white and wing length was retained in our best-performing statistical model, but the effect of tail white was not statistically significant (Fig. 4). If this relationship is true, then tail white may differentially serve as a signal of male condition (body mass) for smaller individuals that may be difficult to assess using other cues, such as structural size. We did not find a relationship between parasitemia and the area of tail white. While our repeatability measurements suggest consistency across replicated samples, we see low repeatability within each parasite genus. The lack of a significant relationship between parasitemia and the area of tail white may thus reflect error associated with our estimates of parasitemia, or the lack of a relationship between tail white and levels of parasitemia.

In conclusion, we found that the size of tail white patches in male Cerulean Warblers was a good predictor of age and structural size (by wing length), and that tail white may also predict body mass in structurally smaller males (estimated by wing length). These results are consistent with tail white patches signaling some, but not all, aspects of quality in male Cerulean Warblers; however, we lack information on whether other Cerulean Warblers perceive or use this information. We require future experimental studies to know if variation in tail white is perceived and used to inform behavioral interactions among Cerulean Warblers on their breeding grounds, or elsewhere.

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APPENDIX 1. Top-performing models ( $\Delta AICc < 2$ ) testing if the area of tail white ( $\text{mm}^2$ ) varies with structural size (estimated by wing and tarsus length) in male Cerulean Warblers (*Setophaga cerulea*). Top-performing models were identified from model fit comparisons that included all possible combinations of predictor variables.

Int <sup>a,b</sup>	A	T	Wg	A × T	A × Wg	df	AICc	$\Delta AICc$	weight
-310.9	+		8.05			4	733.7	0.00	0.26
-326.5	+	4.35	7.21	+		6	734.7	0.94	0.16
-445.8	+		10.02		+	5	735.0	1.33	0.13
-428.5	+	10.16	7.29			5	735.1	1.39	0.13
-479.2	+	3.032	9.77	+	+	7	735.5	1.76	0.12
239.1	+					3	735.6	1.87	0.10
104.6	+	8.072		+		5	735.6	1.92	0.10

<sup>a</sup> Abbreviations: Int = Intercept, A = Age class (second-year or after-second-year), T = Tarsus length, and Wg = Wing length.  
<sup>b</sup> Numbers for predictor variables are effect sizes.

APPENDIX 2. Top-performing models ( $\Delta AIC_c < 2$ ) testing if body mass (g) varies with the area of tail white ( $\text{mm}^2$ ) in male Cerulean Warblers (*Setophaga cerulea*). Top-performing models were identified from model fit comparisons that included all possible combinations of predictor variables.

Int <sup>a,b</sup>	A	T	Wh	Wg	A × T	A × Wh	A × Wg	T × Wg	Wh × Wg	df	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	wt
-17.1	+	0.15	0.097	0.35	+		+		-0.001	10	76.2	0.00	0.23
-23.4			0.12	0.48					-0.002	6	76.7	0.55	0.18
-29.0	+	0.11	0.13	0.53	+				-0.002	9	77.0	0.86	0.15
-40.9	+		0.20	0.73		+			-0.003	8	77.2	1.07	0.14
5.62	+	0.17	0.003	0.01	+		+			9	77.5	1.37	0.12
-112.4	+	6.05	0.087	1.74	+		+	-0.09	-0.001	11	77.8	1.65	0.10
-127.7	+	8.20	0.003	1.95	+		+	-0.12		10	78.1	1.97	0.09

<sup>a</sup> Abbreviations: Int = Intercept, A = Age class (second-year or after-second-year), T = Tarsus length, Wh = Area of tail white, Wg = Wing length, and wt = weight.

<sup>b</sup> Numbers for predictor variables are effect sizes.