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Variation in plumage reflects avian habitat associations not revealed by abundance

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ABSTRACT—For bird species in which plumage characteristics are associated with social dominance, the analysis of status badges may reveal habitat preferences. We analyzed the extent of male Chestnut-sided Warbler (*Setophaga pensylvanica*) chestnut-colored plumage in relation to age and body size to determine whether badge size was a potential indicator of resource-holding potential. We then modeled badge size in relation to habitat variables including habitat patch size, patch shape, and microhabitat characteristics in 101 different silvicultural openings in western Massachusetts during 2014 and 2015. Overall, older and larger Chestnut-sided Warblers had larger badges. Badge size showed a strong positive relationship with patch area. Notably, our findings reveal a greater sensitivity to area than was apparent from a different study's analysis of abundance at the same study site during the same time period. Badge size was positively related to patch shape complexity—an environmental variable not previously identified as important for this species by other studies. Our findings indicate that remote assessments of avian status badges may serve as reliable indicators of habitat preferences and suggest that this approach has the potential to reveal responses to gradients in habitat not reflected by abundance. *Received 11 March 2018. Accepted 17 November 2018.*

Key words: abundance, area-sensitivity, Chestnut-sided Warbler, patch shape, plumage, status badge

La variación en el plumaje refleja asociaciones de aves y sus hábitats que no son reveladas por la abundancia

RESUMEN (Spanish)—Para aquellas especies de aves en las que las características del plumaje están asociadas con su dominancia social, el análisis de distintivos de estatus podría revelar preferencias de hábitat. Analizamos qué tan extenso es el plumaje color castaño del chipe *Setophaga pensylvanica* en relación con la edad y el tamaño corporal para determinar si el tamaño de su distintivo de estatus es un indicador de su potencial para disponer de recursos. Durante 2014 y 2015, modelamos el tamaño del distintivo y su relación con variables del hábitat que incluían el tamaño del parche de hábitat, la forma de éste y las características del microhábitat en 101 diferentes claros de silvicultura en el occidente de Massachusetts. En general, los *S. pensylvanica* más viejos y más grandes tenían distintivos más grandes. El tamaño del distintivo mostró una fuerte relación positiva con el área del parche de hábitat. Es de destacar nuestros hallazgos revelan una mayor sensibilidad al área de la que fue encontrada en un análisis de abundancia en un estudio independiente que se llevó a cabo en el mismo sitio de estudio durante el mismo periodo de tiempo. El tamaño del distintivo estuvo positivamente relacionado con la complejidad de la forma del parche de hábitat—una variable que no había sido identificada en otros estudios como de importancia para esta especie. Nuestros hallazgos indican que la determinación remota de los distintivos de estatus en aves podría servir como un indicador confiable de preferencias de hábitat y sugieren que este enfoque tiene el potencial de revelar respuestas a gradientes de hábitat que no son reflejadas por la abundancia.

Palabras clave: abundancia, distintivo de estatus, forma del parche de hábitat, plumaje, sensibilidad a área, *Setophaga pensylvanica*

Habitat characteristics associated with elevated survival and reproduction are considered higher quality (Van Horne 1983, Johnson 2007, Beerens et al. 2015). Robust assessments of avian survival and reproduction can be time-consuming and costly (Pidgeon et al. 2006). For this reason, researchers often rely on abundance as an efficient indicator of habitat quality (Rudnicky and Hunter 1993, Schlossberg and King 2008, Perry and Thill 2013). The underlying assumption of these studies is that individual birds can identify and select habitat according to its potential to improve survival or reproduction, and as a result, abundance is positively correlated with habitat quality (Johnson 2007). Although this is generally true (Bock and Jones 2004), there are numerous accounts of populations in which density is greater in lower-quality habitat (Van Horne 1983, Vickery et al. 1992, Pidgeon et al. 2006)—particularly in habitats that are highly variable in space and time and species that exhibit pronounced social hierarchies such that dominant individuals displace subordinate males into marginal habitats (Van Horne 1983, Bock and Jones 2004).

Status badges (Krebs and Dawkins 1984, Hill 1991), which are typically conveyed through the size (Dunn et al. 2010) or coloration (Garcia-Navas et al. 2012) of certain plumage characteristics, are a common way for birds to signal fighting ability (Enquist 1985, Senar 2006) and therefore resource-holding potential (Laubach et al. 2013). If a badge is an honest (Jawor and Breitwisch 2003) indicator of resource-holding potential, males with the largest or most colorful badges should maintain territories within the highest-quality habitat in any given locality (Enquist 1985). Thus, proven status badges—that

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can be easily assessed in the field—are one potential method by which to make inferences about a species' relationship with the environment (Reudnick et al. 2009, Germain et al. 2010) irrespective of abundance.

Many shrubland bird species are considered "area-sensitive" because they are less abundant in, or absent from, small patches of habitat (Schlossberg and King 2007). Several shrubland species also show negative edge effects (Schlossberg and King 2008), which are heightened in smaller patches due to greater edge–area ratios. Still, some declining shrubland-obligate species (Sauer et al. 2014), such as the Chestnut-sided Warbler (*Setophaga pensylvanica*), have shown no detectable aversion to edges (Schlossberg and King 2008) and readily occupy forest openings <0.3 ha in size (Roberts and King 2017), suggesting relatively low thresholds of area-sensitivity. If larger patches provide higher-quality habitat and thereby a greater advantage (reproductive or otherwise), the strongest and most experienced individuals—as signaled by the largest badges—should be present in more expansive patches.

Attempts to directly assess the impact of patch shape on birds using abundance have failed to reveal clear relationships—negative or positive—for shrubland species (Chandler et al. 2009, Shake et al. 2012, Roberts and King 2017). This lack of evidence may indicate that shrubland birds are generally indifferent to patch shape, but it is also possible that abundance as a metric may be ill suited for the examination of this relationship. For instance, irregular and uniform patches of the same size may support the same number of birds, but competition may be more intense for one end of the shape complexity spectrum over the other. Birds may compete for more uniform patches because irregular patches increase proximity to edge habitat, which may increase nest predation rates (Shake et al. 2011). If a preference related to shape complexity does exist, variation in status badge may offer a more appropriate metric for examining this relationship.

In a study of area thresholds of songbirds in shrubland patches, we reported several species increased in abundance with increasing patch area (Roberts and King 2017). One of these species, the Chestnut-sided Warbler, exhibits substantial variation in the streak of chestnut-colored feathers extending from the neck along the flank toward the undertail coverts. This plumage characteristic has been suggested as a possible status badge (Richardson and Brauning 1995) and has been shown to have strong positive associations with nest initiation (King et al. 2001) and provisioning rates (Belinsky 2008). The existence of this species across what appears to be a gradient of habitat quality presents the opportunity to examine whether badge size is associated with habitat quality. The objectives of this study were to (1) identify whether the chestnut flank coloration of Chestnut-sided Warblers functions as a potential signal of male resource-holding potential, as indicated by the results of previous studies (King et al. 2001, Belinsky 2008), by assessing its relationship with age (Marra 2000, Rohwer 2004) and body size (Candolin and Voigt 2001, Laubach et al. 2013), and (2) determine whether there is a relationship between badge size and habitat characteristics such as patch area, patch shape, and microhabitat variables. We expected that if patch area, shape, and certain microhabitat characteristics are associated with habitat quality, as is suggested by the published literature (King and DeGraaf 2004, Schlossberg and King 2008, Schlossberg et al. 2010), then Chestnut-sided Warblers with smaller badges will be concentrated in habitats considered lower quality (e.g., smaller habitat patches).

Methods

Study area

We conducted this study in 2014 and 2015 in a largely forested area (>90%) of western Massachusetts (42.5°N, 72.3°W; Fig. 1). Mature tree species primarily consisted of red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), black birch (*Betula lenta*), American beech (*Fagus grandifolia*), red oak (*Quercus rubra*), and white pine (*Pinus strobus*). Birds were studied in 101 forest canopy openings, the majority of which were created with group selection, an uneven-aged management strategy where groups of trees are removed from a mature forest matrix (Smith et al. 1997). Forest openings were created 4–8 yr prior to sampling and ranged in size from 0.04 to 1.29 ha. Vegetation within openings consisted primarily of birches (*Betula* spp.), white pine, red maple, *Rubus* spp., mountain laurel (*Kalmia latifolia*), and fern species.

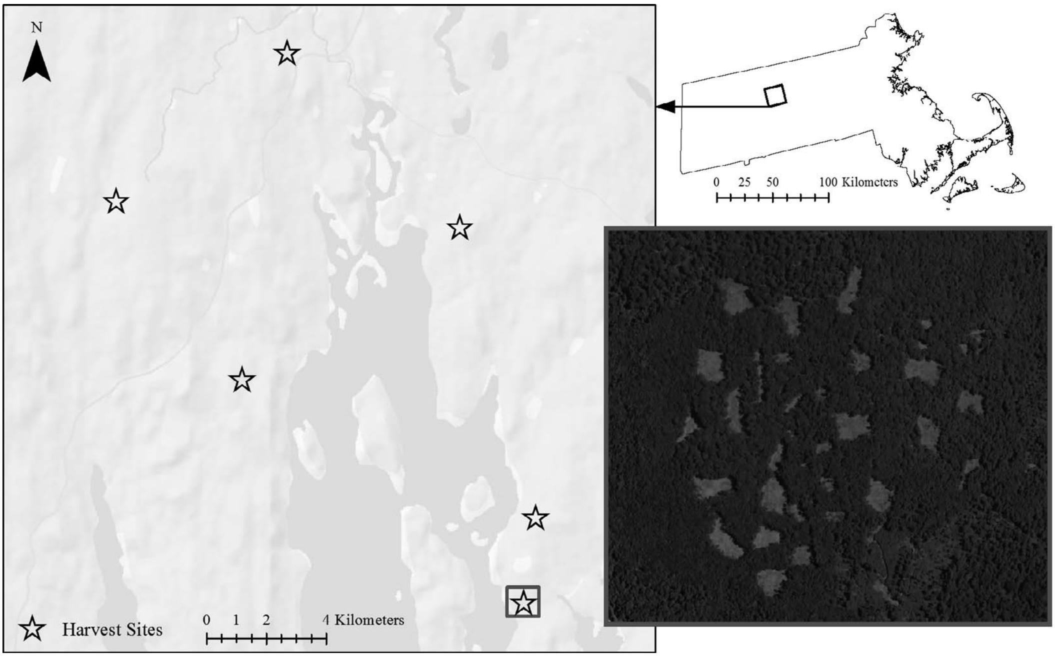

Figure 1. Map of study area in western Massachusetts (42.46°N, 72.32°W). Black stars indicate harvest sites where birds were observed and captured. The smaller rectangle shows an aerial view of one of the 6 sites in the study.

Bird measurements and remote badge assessments

We captured a subset of male Chestnut-sided Warblers from 12 May to 12 June using digital song recordings and mist nets. We banded each bird with a U.S. Geological Survey aluminum band and a unique color band combination (for the purposes of a separate study). We measured wing chord, tail length, and tarsus length using a ruler or mechanical calipers. We measured mass using a digital scale. We determined sex using methods described by Pyle (1997), the presence of a cloacal protuberance (Morton 2002), or the observation of singing post-capture (on rare occasions). We aged birds as second-year (SY) or after-second-year (ASY) by assessing plumage (Pyle 1997) and molt-limits. Birds were only measured once during the study. Capture and processing of birds was approved by the University of Massachusetts Institutional Animal Care and Use Committee (protocol number: 2014-0020).

We assessed the badge of male Chestnut-sided Warblers using binoculars (8-power) in early July of each year. We scored the extent of chestnut plumage on a single side (right or left) of individuals once per year. We gave individual birds a score corresponding to the approximate proportion of the flank containing chestnut feathers. We gave a score of 1 to birds if the badge extended from the neck past the legs (nearly to the under-tail coverts; Fig. 2), 0.75 if the badge extended to the legs, 0.66 if the badge ended just before the legs, 0.5 if the badge was roughly half of a full badge, 0.33 if the badge extended to between the wing bars (white stripes on the wing coverts), and 0.25 if the badge was restricted to before the first wing bar. We only recorded scores if the entire flank was observed. We collected badge information from Chestnut-sided Warblers in 101 openings across 6 sites (Fig. 1). We only collected data for males that were singing within openings. While smaller openings typically only contained one individual, larger openings in this study provided habitat for >1. We avoided double-counting individuals by carefully observing territories when >1 birds were in a single opening and collecting all badges during a single visit to each opening. To inform the accuracy of binocular-based measurements, we assessed badges on each individual's right flank during the banding process

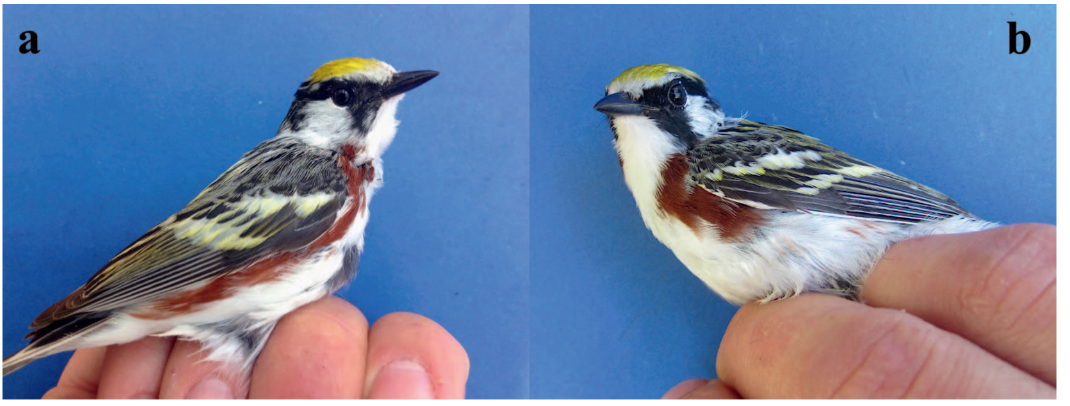

Figure 2. Chestnut-sided Warblers captured during this study with large (a) and small (b) chestnut badges.

using the same scoring criteria. Although this approach for scoring badge size was less precise than more intensive methods (e.g., Laubach et al. 2013), our validation of the remote assessment with binoculars with data from captured birds, as well as the assignment of plumage scores to 2 categories for analyses (see below), minimized the influence of any imprecision on the results.

Vegetation surveys

We measured vegetation at 20 random locations in each opening using random bearings and distances (1–25 m) and starting from the middle of each opening, following Roberts and King (2017). At each location, we placed a pole perpendicular to the ground and recorded the plant species and maximum height of plants touching the pole within 4 height classes: 0–0.49 m, 0.5–1.39 m, 1.4–2.9 m, and >3.0 m (Martin et al. 1997).

Statistical analysis

We obtained a single badge score representing each opening by calculating the average badge score of all birds detected within each opening. We did not model individual badge scores because a substantial proportion of openings contained >1 territory, raising the issue of pseudoreplication (Hurlbert 1984). We did not add a site effect because, with 101 sites, it would have resulted in overfitting of models due to a large variable-to-sample-size ratio. An alternative would have been to model only the largest badge in each opening; however, potential patterns of badge-specific patch occupancy with respect to area might have been obscured if, for example, birds with large badges occupied most openings, but openings at one end of the area gradient also hosted birds with smaller badges. Furthermore, only including the largest badge per opening in the analysis would have prevented us from analyzing badge-specific differences in microhabitat associations. Regardless, our use of the average badge size most likely had little effect on the analysis because approximately two-thirds of openings with >1 bird were occupied by birds with the same badge size.

Badge size per opening was left-skewed and showed a bimodal tendency reflecting no established distribution. This pattern was similar to that observed by Belinsky (2008). Because this distribution made adhering to known modeling framework assumptions difficult, we represented badge as a binary variable reflecting each mode of the bimodal distribution. We gave openings a score of 0 if the average badge was small, scoring <0.75, and a score of 1 if the average badge was large, scoring ≥0.75. We used this cutoff because it represented a clear divide between the 2 modes of the distribution.

We performed a principal component analysis (PCA) on wing chord, tail length, and tarsus length to obtain a single variable representing body size. Weight was not included in this calculation because we caught birds over the course of a month during which time males could have been at different points in their breeding cycle and thus vary considerably in weight. The first principal component accounted for 47% of the variance (loadings: wing chord –0.67, tail length –0.71, tarsus length –0.21). We used the equation for this component to calculate the principal component scores for birds with all 3 measurements. We employed logistic regression models to relate badge size to body size and age. We fit a model containing both age and body size to determine whether body size was still a strong predictor when controlling for age. We fit models using the glm function in the "stats" package (R Core Team 2014) in the R software environment, version 3.1.1.

We employed logistic regression to relate badge size to environmental variables. The predictor variables considered in habitat models were percent cover of broadleaf shrubs and saplings, percent cover of needleleaf shrubs and saplings, percent cover of herbaceous vegetation, median vegetation height, coefficient of variation of vegetation height, patch area, and patch shape. These variables are known or suspected to be important for shrubland birds (Schlossberg et al. 2010, Roberts and King 2017). We considered all variables for model selection because correlation coefficients were never >0.7. We included a covariate for year in all models. We used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to compare and rank models. We used the MuMIn package (Barton 2016) in R to compare models containing all subsets of variables with the condition that no model could have more than 4 predictor variables. This limit was placed on models to prevent overfitting. We considered variables supported if present in models with $\Delta AIC \leq 2$ (Burnham and Anderson 2002) and strongly supported if 95% confidence intervals (CI) of β estimates did not include 0. To visually represent the relationship between badge size and area, we plotted the weighted-average (using Akaike weights [Burnham and Anderson 2002]) predictions for all models with $\Delta AIC \leq 2$ (following Roberts and King 2017). In this process, we kept all environmental variables other than area at their mean. Because year was a strong predictor, predictions were plotted for each year.

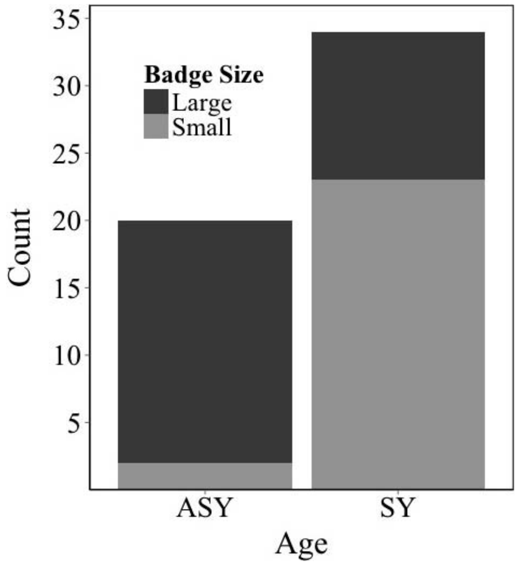

Figure 3. Relative proportion of badge sizes within after-second-year (ASY) and second-year (SY) age classes. Birds were caught in 2014 and 2015 in forest openings created by group selection harvests in western Massachusetts, USA.

Results

We caught 53 male Chestnut-sided Warblers in 2014 and 21 in 2015. Twenty-one of these birds were ASY, and 34 were SY; we were unable to age the remaining 19 individuals. Seven of 74 males captured had different in-hand badge scores from binocular-based scores, 4 of which would have changed the individual's score from "small" to "large" or vice versa. Models using binocular-based scores indicated that large badges were representative of older (Fig. 3) as well as larger birds (as indicated by non-overlap of confidence intervals with zero), regardless of age (Table 1).

We scored badges of 87 birds in 63 openings in 2014 and 103 birds in 72 openings in 2015. There was a strong and consistent positive relationship between badge size and patch area in all top models (Table 2; Fig. 4) as indicated by non-overlap of confidence intervals with zero. Badge size displayed a negative relationship with forbs, ferns, and grasses (2 of 3 models) and a positive relationship with patch shape (2 of 3 models), but 95% CI of coefficients included zero. Year was a strong predictor in all models, with more birds having large badges in 2015 overall.

Discussion

This study provides evidence that the Chestnut-sided Warbler's chestnut-colored flank may func-

Table 1. Results of generalized linear models relating badge size to age, body size, and individual body measurements. Asterisks indicate coefficients with 95% confidence intervals that do not include zero.

				95% CI	
Variable(s)	*n*	β	SE	Lower	Upper
Age[a]	54	−3.25*	0.88	−5.29	−1.71
Body size[b]	62	−0.67*	0.27	−1.26	−0.18
Age + Body size[b]	46	−4.07*	1.28	−7.28	−1.96
		−0.86*	0.47	−0.03	−1.91

[a] Second-year or after-second-year. Negative coefficients indicate positive relationship with age.
[b] Principal component axis representing wing, tail, and tarsus length. Negative coefficients indicate a positive association with body size.

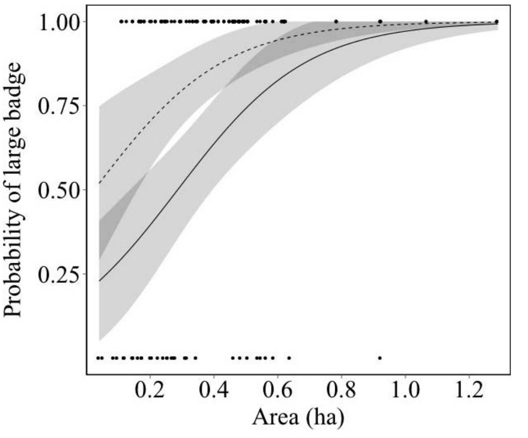

Figure 4. The probability of a large badge (averaged across all birds in an opening) in relation to patch area in 2014 (solid line) and 2015 (dashed line). We show the weighted-average predictions for the best-performing models (difference in Akaike's Information Criterion ≤2). Shaded areas represent 95% confidence intervals. Patch area was a strong predictor (95% confidence intervals did not include zero) in all top models. Data comes from surveys conducted in forest openings in western Massachusetts, USA.

tion as a status badge, signaling older and larger birds. Generally, older passerines are thought to be more dominant and likely to win contests (Hurd and Enquist 2005) and studies have reported that plumage badges are an effective predictor of aggressiveness for certain species (Studd and Robertson 1985, Møller 1987, Lemel and Wallin 1993). Therefore, the extent of chestnut present on individuals may serve as a method for conveying subordinance (Lyon and Montgomerie 1986) to avert aggressive interactions. Indeed, we witnessed males lowering their wings such that the full extent of their badge could not easily be seen, which may have been strategic behavior intended to avoid aggressive encounters. Our finding that badge size was an effective predictor of body size, even when age was included in models, indicates that badge size may be an honest indicator of resource-holding potential (Laubach et al. 2013), irrespective of age. Because the Chestnut-sided Warbler's badge appears to serve as a reliable indicator of both age and resource-holding potential, in cases where habitats vary in quality, individuals with the largest badges should defend territories in the most preferred habitats.

Table 2. Candidate generalized linear models representing the relationship between badge size and habitat characteristics. Asterisks indicate coefficients with 95% confidence intervals that do not overlap zero. Superscript numbers indicate the largest % CI for that coefficient that does not include zero. Year is included in all models, but not provided.

Area	FFG[a]	Shape[b]	ΔAIC[c]	w_i[d]
5.05*	-3.19^{93}	2.62^{94}	0	0.51
4.63*		2.54^{93}	1.34	0.26
5.07*	-3.09^{92}		1.65	0.23

[a] Percent cover of forbs, ferns, and grasses.
[b] Shape complexity (patch perimeter divided by the minimum possible perimeter of a patch equal in area).
[c] We only show models with ΔAIC ≤ 2.
[d] Akaike model weight.

Our observation that badge size was related to several habitat characteristics is consistent with the hypothesis that this plumage feature may serve as an effective indicator of habitat preference in Chestnut-sided Warblers. Our findings show a greater sensitivity to patch area than had been revealed by analyses of abundance alone. Prior research reported that the patch size for which there was a 0.9 probability of Chestnut-sided Warbler occurrence was 0.28 ha (Roberts and King 2017). In contrast, our weighted-average model predictions of the probability of a large badge did not reach 0.9 until 0.48 ha in 2015 and 0.72 ha in 2014, showing a continued response to patch size beyond what was revealed by abundance. The findings of King and DeGraaf (2004) suggest that larger forest openings confer an advantage with respect to nesting success, with birds in larger openings initiating nesting earlier, giving them more time to renest in the event of nest failure. Larger openings may provide other benefits such as increased food resources (DeGraaf and Yamasaki 2003), which may in turn improve the condition and survival of nestlings (Clutton-Brock 1991), greater chances for extrapair copulation (Byers et al. 2004), or more cover for offspring during the vulnerable post-fledging period (King et al. 2006).

Our observation that badge size was negatively associated with the presence of forbs, ferns, and grasses is consistent with findings by Schlossberg et al. (2010) as well as Chandler (2006) that the abundance of Chestnut-sided Warblers was negatively associated with the cover of herbaceous growth, suggesting these habitats are less preferred. This may be due to the fact that herbaceous vegetation was negatively correlated with shrub cover at our sites ($P < 0.05$). Chestnut-sided Warbler abundance is typically associated with low, woody cover (Hagan and Meehan 2002, King et al. 2009, Smetzer et al. 2014), probably because they nest in shrubs and small saplings (Schill and Yahner 2009) and sites with extensive shrub cover provide more options for nest sites. Woody stem density is also reported to be associated with higher nest survival (Schill and Yahner 2009).

The positive association of larger-badged birds (which tended to be older) with irregularly shaped openings contrasts with Roberts and King (2017), who failed to detect a relationship between shape complexity and abundance (at the same study site during the same years), but is consistent with Weldon and Haddad (2005) who reported that older ASY Indigo Buntings (*Passerina cyanea*), a shrubland species (Schlossberg and King 2007), preferred more irregular patches. Presumably this positive association is an indication that, contrary to previous speculations (Schlossberg and King 2008), shape complexity may confer greater habitat quality for some shrubland species, although it is less clear how this increased quality is manifested, or under what conditions. It is possible, as suggested by Weldon and Haddad (2005), that complex patches—when situated within mature forest—may offer more prominent song posts from which to defend territories (also see Kroodsma 1984). Despite the observed preference for irregular patches, greater proximity to edge habitats may lead to reduced nesting success (Shake et al. 2011). Indeed, Weldon and Haddad (2005) suggested that by both attracting ASY males and facilitating lower reproductive success, irregular openings may function as ecological traps for Indigo Buntings. However, King and DeGraaf (2004) found no relationship between Chestnut-sided Warbler reproductive success and shape of silvicultural openings in New Hampshire, suggesting that irregular openings may not serve as ecological traps for Chestnut-sided Warblers. Irregular and uniform openings in this study supported roughly the same number of individuals, but may have experienced different levels of competition, as reflected by the variation in badge size, making it a more effective metric for examining this variable.

Our findings suggest that gradients in habitat quality may exist that are not readily detectible using measures of abundance alone. The shortcomings of abundance as an indicator of habitat quality are widely recognized (Van Horne 1983), but alternative metrics of habitat quality, such as nest success, require substantial investments of field time. These results illustrate the potential for badge measurements—when readily observable—to supplement abundance estimates in ecological studies that focus on habitat quality. Within our study area, the most abundant species, such as Prairie Warbler (*Setophaga discolor*), Common Yellowthroat (*Geothylpis trichas*), and Eastern Towhee (*Pipilo erythrophthalmus*), exhibit variation in certain plumage characteristics that may serve as status signals (e.g., Freeman-Gallant et al. 2010). As opposed to measuring survival or reproduction, status badges may represent a relatively efficient way of providing support (or lack thereof) for the assumption that abundance is positively correlated with habitat quality. However, it should be noted that while remote status badge assessments appear to present a unique lens through which to assess habitat quality, further research is clearly needed to both determine the feasibility of this approach for other species with differing badges and refine best methods for badge assessment.

Conclusion

We demonstrate that, for species in which plumage characteristics are variable and associated with social dominance, remote assessments of plumage traits may serve as effective measures of habitat preferences. This was evidenced by the confirmation of 2 previously identified relationships with patch area and non-woody plants, which have been linked to increased reproductive success (King and DeGraaf 2004, Schill and Yahner 2009). Our observation of a continued preference for larger patches of habitat by Chestnut-sided Warblers beyond the threshold reported by Roberts and King (2017) suggests that badge assessments may help refine our understanding of known habitat relationships. Our finding that patch shape complexity was related to badge size, despite being unrelated to abundance at the same sites (Roberts and King 2017), emphasizes the potential for this methodology to reveal previously unidentified associations. Status badges, if proven to be honest (Jawor and Breitwisch 2003), may offer an additional tool for managers interested in rapid and relatively inexpensive methods to augment habitat evaluations based on abundance.

Acknowledgments

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