

Clarifying Spotted Towhee subspecies in the Nebraska panhandle and the need for scientific studies on a phenotypic cline



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Subspecies are meaningful and useful taxonomic categories used to classify biodiversity. If breeding populations within a species can be reliably divided into distinct, biologically meaningful units (Patten 2010, Van Remsen 2010) and if these units are exposed to different selective pressures related to survival, then increased understanding and consensus on the distribution, life-history characteristics, and identification of these population units is essential.

Assuming that any reasonable definition of a subspecies includes an element of geography and a diagnostic physical characteristic(s) based on heritability (Patten 2015), field identification should be both possible based on at least one diagnostic trait and said diagnostic trait should correspond to a population that occupies a meaningful geography distinct from others within the species. From the perspective of field ornithology, subspecific identification therefore must be made based on an observable trait(s). Ideally, observable traits have been tested through additional scientific study (i.e. genetics, specimens or individual tracking) to affirm the relevancy to distinct geographical and biological units. The reliability and relevance of subspecific identification has arguably never been more pertinent, as subspecific identification of field observations in the global citizen-science platform eBird (eBird.org) continue to increase and expand.

Even within well-studied populations, the distinctiveness of avian subspecies is often variable. Certain subspecies fulfill all basic criteria including readily identifiable diagnostic traits that correspond to breeding geography where contact zones are either non-existent (e.g., Grasshopper Sparrow; Vickery 2020), small and stable (e.g. Yellow-rumped Warbler; Bresford and Irwin 2009), or held in tension by assortative mating or strong selection against hybrids due to migratory divides (e.g. Swainson's Thrush; Delmore et al. 2012). Usually within these clear-cut cases, there is genetic distinction, and several recent examples are precursors to the elevation to species level (e.g. Eastern Warbling-Vireo/Western Warbling Vireo, Stejneger's Scoter/White-winged Scoter).

As is often the case in ecology, unambiguous examples that adhere to clear concepts are the exception, not the rule. For many subspecies classifications and subsequent identifications, one or more criteria is often excluded, not applicable, or ignored. This is best described by subspecies whose distinguishing trait(s) exist on a continuum across a geographic cline, where extreme ends of the distribution exhibit distinct, readily identifiable traits. Between the extremes the distinguishing phenotypic traits are subtle, with individuals in the 'middle' populations exhibiting intermediate features. Furthermore, many proposed subspecies have not been studied in depth, especially in clinal zones, and the relationships between plumage characteristics, genetics and breeding geography are poorly known and untested. Thus, there is a clear need for additional scientific study that uses repeatable methods and empirical data focused on clarifying subspecific distributions.

We evaluated if field identifiable and measurable phenotypic and morphological traits differ in male Spotted Towhees (*Pipilo maculatus*) in a likely clinal contact zone in the western Great Plains. We tested assumptions that multiple purported subspecies occur within in the region during the breeding season, as has been reported. We also evaluated the reliability of proposed field marks that have been suggested to be diagnostic traits used to distinguish birds of two different subspecies. By testing the reliability of proposed traits for field identification between potentially co-occurring subspecies, the null hypothesis in our study is that the morphological and phenotypic differences within Spotted Towhees in the western Great Plains are either non-existent or small and variable as to be imperceptible or unreliable using traditional means of field identification.

METHODS

Study Species

Spotted Towhees breed throughout much of western North America and in isolated habitats in Mexico and as far south as Guatemala (Bartos Smith and Greenlaw 2020). As many as 21 subspecies have been recognized (AOU 1957) and these subspecies have been aggregated into five groups by eBird. One monotypic subspecies group is *P.m. arcticus* (hereafter *arcticus*) that breeds in the Great Plains (Fig. 1). *Arcticus* is the subspecies that reportedly breeds in western Nebraska (AOU 1957; Bartos Smith and Greenlaw 2020, Sharpe et al. 2001). The “maculatus group” includes 12 different subspecies that breed in western mountain regions from interior British Columbia to Guatemala (Bartos Smith and Greenlaw 2020). *P.m. montanus* (hereafter *montanus*) is the subspecies included in the “maculatus group” that breeds in central and western Colorado and Wyoming. Both *arcticus* and *montanus* have recently been reported to occur in the Nebraska panhandle during migration and breeding periods and in adjacent states of Colorado and Wyoming (Silcock and Jorgensen 2025a, eBird.org) where contact with *arcticus* is likely.

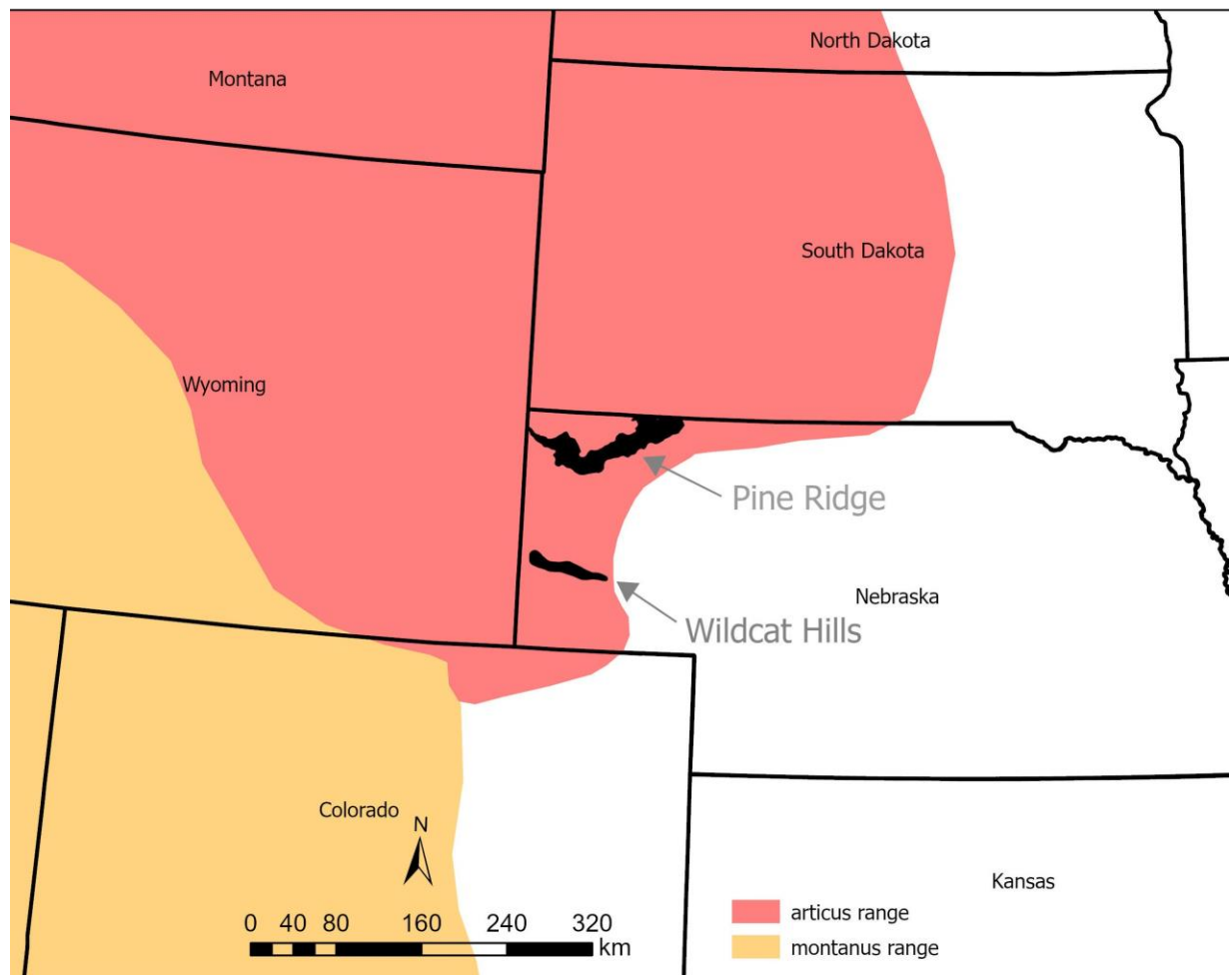


Figure 1. Distribution of proposed Spotted Towhee subspecies relative to two major ponderosa pine dominated escarpments (Pine Ridge and Wildcat Hills) of the Nebraska panhandle. Distribution based on information from Bartos Smith and Greenlaw (2020).

Study Area

The Nebraska panhandle is a mostly flat to gently rolling landscape that historically was dominated by prairie (Condra 1914). Two escarpments, the Pine Ridge and Wildcat Hills, are areas of substantial elevation relief that are also the only areas in the panhandle that historically harbor open pine, riparian woodlands, as well as woody understory (Condra 1914, Fig 1). Much of the former prairie has been converted to row-crop agriculture and woody vegetation has expanded because of human activity. However, both historically and presently, the Pine Ridge and Wildcat Hills are two primary regions where Spotted Towhees breed. We captured Spotted Towhees at Gilbert Baker WMA and Fort Robinson WMA in the Pine Ridge and Wildcat Hills SRA and Buffalo Creek WMA in the Wildcat Hills. By containing our study to the extreme west, we were most likely to avoid Eastern Towhee (*Pipilo erythrophthalmus*) features and/or genetic influence (Silcock and Jorgensen 2025b), and these areas are also where all *montanus* records have been reported in the state.

Field Methods

We banded male Spotted Towhees from 15 May – 10 June in 2024-2025 to examine how phenotypic traits correspond to morphometric characteristics across birds breeding in the panhandle of Nebraska. We chose this time period each year because towhees were on breeding territories and in relatively unworn plumage. We used mist nests centered in territories or along territory boundaries of singing towhees and used conspecific audio playback of various Spotted Towhee calls and songs to capture males. Upon capture, we measured wing-chord, tail length, hind toe (hallux), tail spot on R6, and took a repeatable series of photographs against a neutral background to later assess phenotypic traits (see Fig 2). We aged each bird as either Second-Year (SY) or After-Second Year (ASY) based on a combination of molt, feather wear, feather edge colors, and eye color (Pyle 1997 and 2022, Brenner and McWilliams 2019, Hohn et al. 2025). Birds were banded and released back on territory. We also performed rapid-assessment surveys of habitat at a banded bird's breeding territory estimating percent shrub and canopy cover as well as dominant woody species.

Field identification and Phenotypic scoring

We tested the reliability and validity of subspecific field identification, which in most cases is documented and reported in the eBird online platform (eBird.org). According to multiple field identification sources (Pyle 1997, Nat. Geo. Soc. 2008, Bartos Smith and Greenlaw 2020), visual subspecies identification between these two forms can be based on the length of the tail spot relative to the overall tail size (creating a longer-tailed and smaller spot look in *montanus* relative to *arcticus*) and the amount of white spotting on the dorsum, scapulars, and coverts of males (heavier spotting and more white overall in *arcticus* relative to *montanus*). These phenotypic traits also correspond to nearly distinct morphometric traits, namely larger tails (>104mm) and hind-toe size (>19mm) in *montanus* relative to *arcticus* (Bartos Smith and Greenlaw 2020). To assess the visual impression of dorsal and wing spotting associated with the subspecies identification of *arcticus* and *montanus*, we used a modified plumage scoring system for each individual bird similar to Sibley and West's (1959) study of towhee hybrids in Nebraska, and similar to other plumage scoring systems for hybrids in other *Pipilo* towhees (DeRaad et al. 2023) and orioles (Walsh et al. 2020). Scoring was based on in-hand photographs of male towhees from multiple key angles (Fig 2). We used one author's scoring (SJB) across all individuals to remain consistent and to adhere to previous studies (Walsh et al 2020). We considered the amount and size of white in the coverts, scapulars, dorsum (hereafter referred to as 'spangling') and at the base of the primaries that meet the coverts to score each individual's plumage using the following visual criteria:

Patch at primary base (0-2)

Counting the number of primary shafts where white is visible, using both spread wing and folded wing views.

‘0’ = No or trace white at primary base

‘1’ = Two or less feathers white at base.

‘2’ = Three or more feathers white at base.

Spangling Scoring (0-4)

0=almost none. Approaching EATO or obvious hybrid

1=reduced/half white on largest scapular, minimal to missing white on several covert and scapular feathers

2=largest scapular has moderate to heavy amount of white, but small number (≤ 4) of other scapulars show limited white. Coverts have limited or missing white.

3=mostly full white on largest scapular and large amount of white on multiple other feathers (>4). Most coverts (>6) have large white spots.

4=heavy and large amounts of white on scapular and back feathers, with moderate to large white patches on virtually all coverts (8-9).

These two numeric scores were combined for a visual plumage score ranging from possible 1 – 6 (considering a bird scoring a zero is likely a hybrid). In this case, a ‘1’ would be most consistent with *montanus* features whereas a ‘6’ would be more consistent with an *arcticus*. While the presence, let alone extent, of white in the feather shafts at the base of the primaries is traditionally considered a trait of Eastern Towhees and likely to indicate a hybrid or backcross, birds from our study area have not been examined in-hand for such traits (see Discussion). Regardless of if this mark indicates a functional species-pair hybrid or not, this feature would still be most consistent with birds breeding in the eastern extents of Spotted Towhee distribution, which is always considered the geographic extent of *arcticus* birds.

In addition to visual scoring, we also included the tail spot length relative to the overall tail length (f = total tail length – length of largest tail spot; hereafter tailspot ratio) to account for the impression of shorter tail spots in *montanus* vs *arcticus* towhees. We also analyzed birds using a total phenotype scoring, combining both tail impression and wing spotting impression to encapsulate all visual field marks. To create this score, we first inverted our spangling and wing patch scoring totals so that larger scores would now correspond to *montanus* marks (i.e. less white markings overall is now a score of 6). We then divided all raw tail ratio measurements (mean=64.1mm) by 10 to scale this number to have ~equal weight as the plumage scoring. We then combined the two plumage scores (adjusted tail ratio and inverted visual scoring) to add an additional test that reflects using a combination of visual cues for distinguishing subspecies in the field.

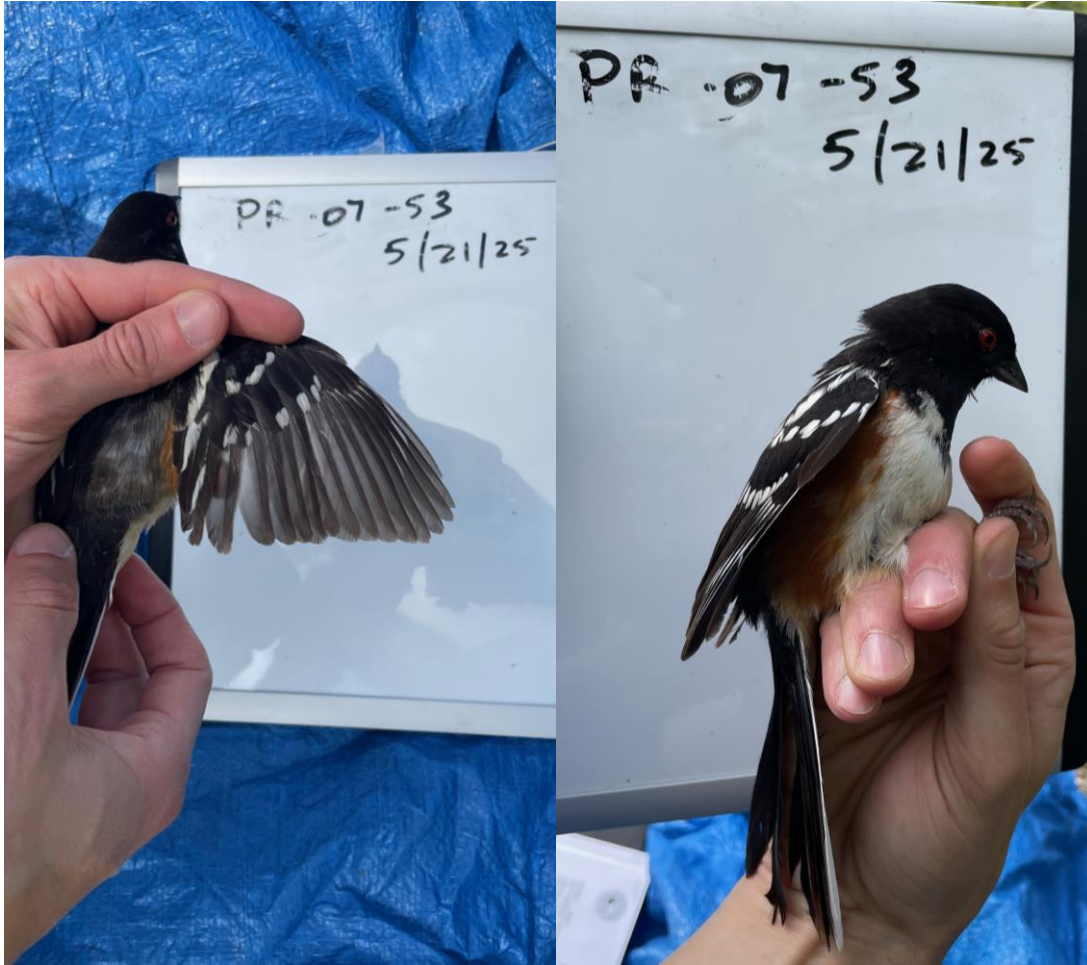


Figure 2. Example of standardized towhee photographs used in this study. This bird would score a '5' of possible 6 for visual spotting. Note that multiple primaries are edged white at the primary base meeting the coverts, visible in spread and folded wing.

We tested the above plumage scoring visual assessments against body morphology to determine if proposed field identifiable visual traits correspond to measurable differences between *montanus* and *arcticus* towhees. We considered hind claw/hallux as the most objective metric of subspecies designation in our study, as this measure has the least amount of reported overlap across other studies and specimens, but in some cases we also considered wing size (Pyle 1997, Bartos Smith and Greenlaw 2020, however see: Pyle 2022). In most testing and models we also used tailspot ratio to assess objective morphological subspecies designation, but not in cases where combined plumage score that includes tail spot was also used. Reported measurements from Pyle (1997) and Bartos Smith and Greenlaw (2020) were used to compare to our measurements of Nebraska panhandle towhees. We used generalized linear models to test various morphological measurements and plumage scoring metrics and used Fisher's Exact test for small sample sizes to compare appearance and plumage measurements between ages and between sites. All statistical testing was done in Program R (R Core Team 2024).

RESULTS

We banded 21 male towhees in the Pine Ridge (n=11) and Wildcat Hills (n=10) from 2024-2025. One towhee was removed from tail-related testing, as it was molting tail feathers upon capture. For all towhees,

phenotype score (5.3-10.3, mean=7.8), tailspot ratio (57-69mm, mean=64.1mm), hallux (14.5-18.1mm, mean=16.2mm), tail (91-102mm, mean=97.7mm) and wing (84-89mm, mean= 85.62mm) were all within reported single standard deviation of *arcticus* measurements (Fig 3). We found that 76% (16 of 21) of male towhees in our study had some white at the base of the primary feathers meeting the coverts.

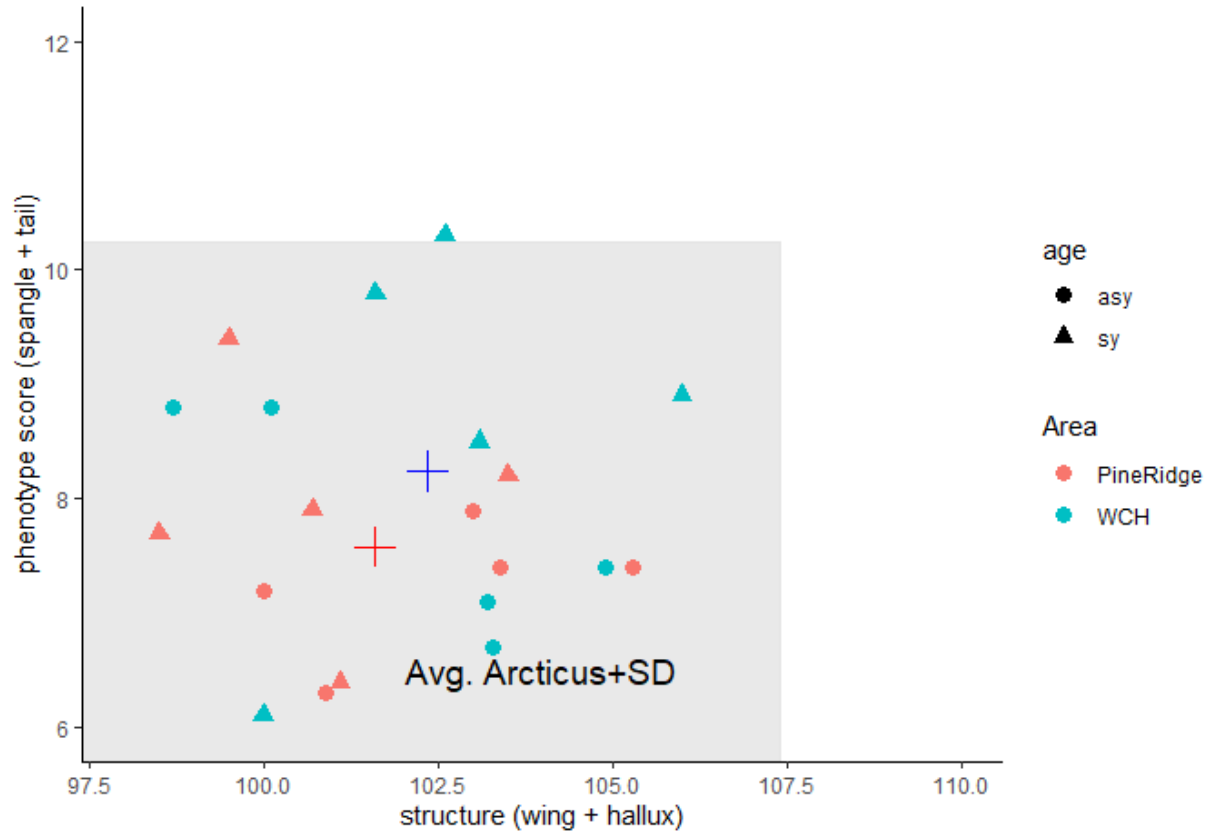


Figure 3. Panhandle Towhee structure by combined phenotype score (tailspot ratio and scapular/wing spotting). Average and standard deviation measurements from specimen and banded *arcticus* towhees (Pyle 1997, Bartos Smith and Greenlaw 2020) are presented as a gray box. Average values from the Pine Ridge (red dots) and Wildcat Hills (blue dots) are presented as red (Pine Ridge) and blue (Wildcat Hills) crosses, with circle (ASY) or triangle (SY) dots corresponding to age.

Male towhee wing size and hallux size were moderately correlated ($R^2 = 0.39$), as was overall tail length and wing ($R^2 = 0.35$). Tailspot ratio and hallux were not related ($\beta = 0.68 \pm 0.74$, $p = 0.37$) and visual score was also not related to hallux ($\beta = 0.01 \pm 0.2$, $p = 0.95$) or tail ratio ($\beta = -0.02 \pm 0.07$, $p = 0.77$). Wing and dorsum plumage score was lower (less white overall) in SY males compared to ASY males ($p = 0.013$) but not different between the Wildcat Hills and Pine Ridge ($p = 0.892$, Fig. 4). Combined phenotype score (tailspot ratio and visual scoring) was not different between ages ($p = 0.124$) and not different between sites ($p = 0.331$). We found no relationships between any habitat metric and any morphological or phenotypic trait in spotted towhees ($p > 0.70$).

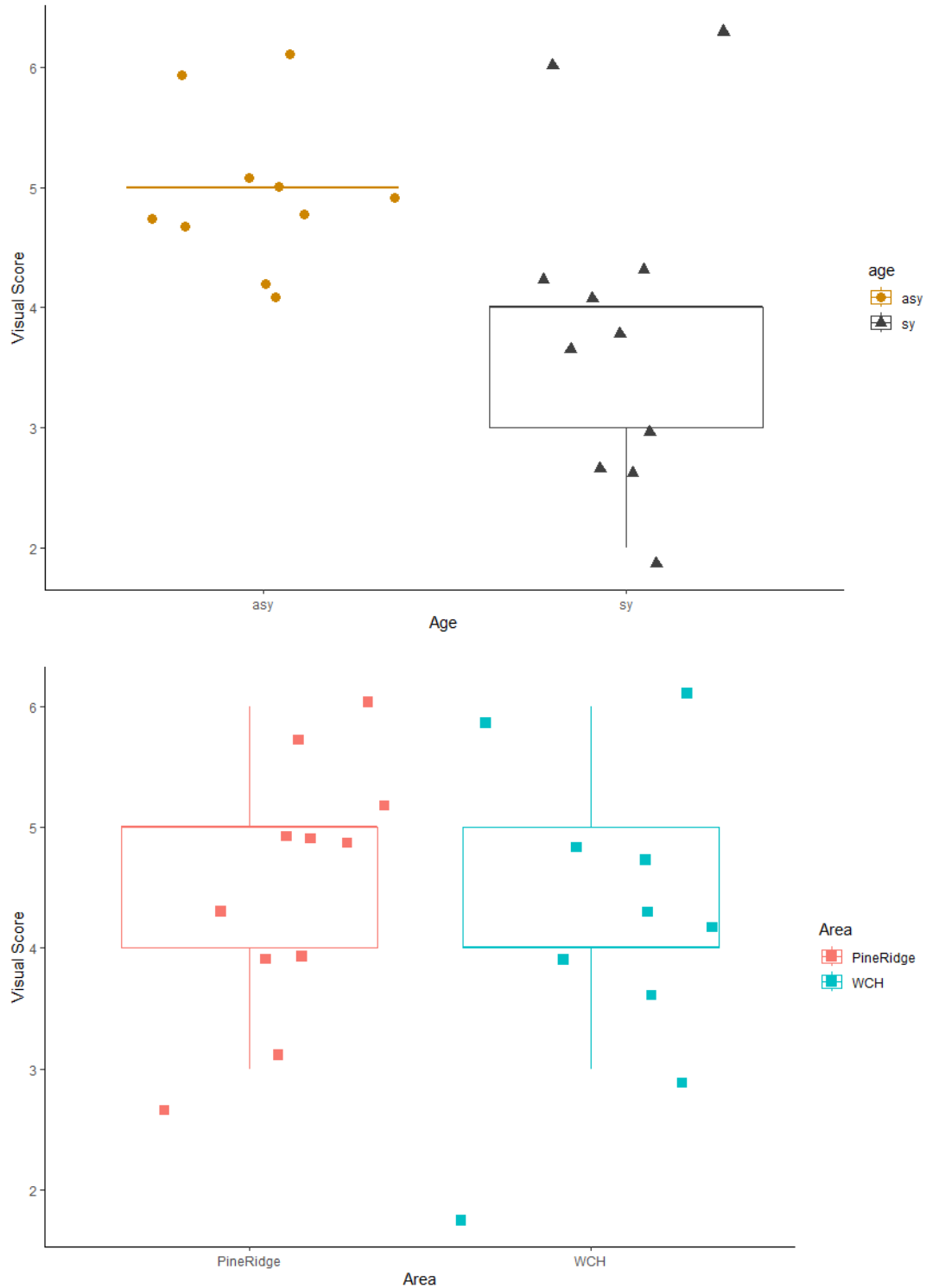


Figure 4. Wing and scapular spotting and spangle score by age (top) and study area (bottom) in male spotted towhees in the panhandle of Nebraska. Boxplot boundaries represent interquartile range (50%) of visual scores by age (top) and area (bottom).

Raw measurements of tailspot ratio and hallux indicate a majority of male towhees (60%, 12 of 20) would be considered *arcticus* based solely on those two measurements, with the remaining birds (n=8) being

unclassifiable on just those two measurements (Fig 5). Male towhees from the Wildcat Hills had average tailspot ratio and hallux measurements of 65.4mm and 16.75mm, respectively, whereas male towhees from the Pine Ridge had slightly lower average tailspot ratio (62.8mm) and hallux measurements (15.79mm), but these did not differ significantly (tailspot: $p = 0.121$, hallux: $p = 0.650$). No sampled birds had any morphometric measurement that would be considered likely or definitively *montanus* (Fig 3, Fig 5).

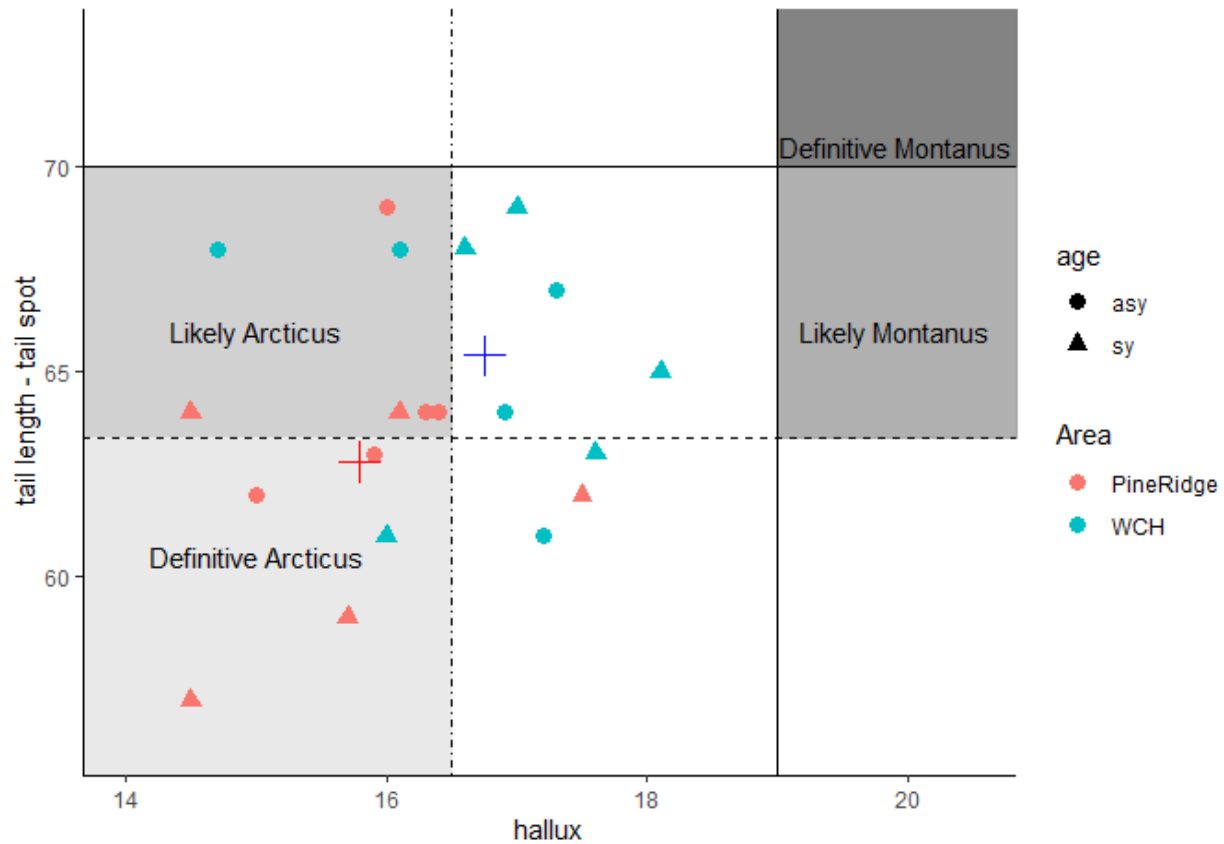


Figure 5. Raw measurements of tailspot ratio and hallux for 20 male towhees in the Nebraska panhandle relative to previously reported measurements from specimen and banded *arcticus* towhees (Pyle 1997, Bartos Smith and Greenlaw 2020; dark and light grey boxes). Average values from the Pine Ridge (red dots) and Wildcat Hills (blue dots) are presented as red (Pine Ridge) and blue (Wildcat Hills) crosses, with circle (ASY) or triangle (SY) dots corresponding to age.

DISCUSSION

We did not find evidence that any other subspecies of Spotted Towhee other than *arcticus* is present during the breeding season and presumably breeds in western Nebraska, consistent with existing literature (AOU 1957, Bartos Smith and Greenlaw 2020, Sharpe et al. 2001). We also did not find support that commonly used visual identification marks are useful in distinguishing individual male towhees of different subspecies near a proposed subspecific boundary or contact zone, nor did we find support for these visual identification marks being diagnostic of any differences between birds morphologically or between populations (i.e. no phenotypic differences between or within sites). We found weak support that some SY male towhees may appear less spotted overall compared to older (≥ 3 year) males within a population. There may be some inherent morphological differences between towhees breeding in the Pine Ridge and those in the Wildcat Hills (Fig 5), but these differences cannot be delineated by previously reported subspecific classifications.

Based on this study, we do not support visually distinguishing towhee subspecies based on previously suggested field marks in western Nebraska or in nearby areas where the distribution of *montanus* and *arcticus* Spotted Towhees transition over a broad geographic area.

Within this broad region of the western Great Plains, we found the most support in our data that apparent visual differences between male towhees of tail spot size and amount of white in the wings and dorsum likely represent individual variation and phenotypic plasticity within a population or cluster of connected populations. We suspect that the apparent difference in the amount of white in the wings and dorsum between SY and ASY males is likely due to feather wear and molt-timing. Scoring is not a precise measurement (e.g. measured length of white in a single feather or covert) but a subjective, albeit consistent, evaluation of appearance, as would be the case for field observation. Thus, worn coverts or molting/missing feathers would create the appearance of less intense white spangling overall. The tails of SY passerines are also typically more worn compared to ASY birds, making the tail spot appear smaller. Additionally, as ~75% of sampled birds had some form of a white patch at primary base, this (a) may not be an entirely consistent mark for Eastern Towhee-Spotted Towhee hybrids, or (b) the amount of introgression of Eastern Towhee genes even in the westernmost Spotted Towhee populations of Nebraska is far more extensive than previously considered.

While certain visual identification marks may be useful to confirm members of different populations and potentially different subspecies at extremes of proposed distributional limits (e.g. southern Arizona vs central Nebraska), we do not support their application near distributional boundaries. It is notable that for structural morphology measurements, ~2mm of hallux and ~7mm of tailspot ratio will definitively separate purported *arcticus* and *montanus* specimens (Fig 5). These are remarkably small margins, especially from a visual observation (photograph or binoculars), let alone from measurements of a bird in hand. Given that 40% (n=8) of our birds were in this small ~14mm² ‘ambiguous’ zone, we suspect that hallux size, tail spot and plumage-related phenotypic traits are clinal in Spotted Towhees. In fact, this has been recently proposed by taxonomic and specimen authorities (Pyle 2025) that now consider *montanus* and *arcticus* synonymous.

While this study was limited in scope (one species) with a relatively small sample size (n=21), these results are the first mensural data for towhee subspecies in the Nebraska panhandle. Therefore, we consider our results a useful case study examining an increasing trend in eBird reporting and within public eBird data. As many of the subspecies groups presented in eBird and in other taxonomies have not been examined in any recent or rigorous manner (i.e. hypothesis-based testing using in-hand, specimen, genetic, or tracking data), we recommend a more cautionary, prosaic approach to subspecies identification capabilities and the ensuing user-driven data until field marks presumed to be useful and diagnostic are rigorously tested with objective, measurable data. Recent examination of many subspecies in North America, particularly those with broad clinal variation, has also suggested that accurate field identification is highly variable and often based on untested assumptions (Pyle 2025).

Spotted Towhees are a relatively secure species. However, in other species, different populations often recognized as subspecies are experiencing divergent population trends (e.g. Bewick’s Wren; Kennedy and White 2020) and emerging challenges as vulnerable environments shift under anthropogenic change (Brenner and Jorgensen 2023). The understanding of the functional ecology of distinct populations and the potential conservation value of delineating or tracking subspecies distributions could be diluted by over-reporting misunderstood or untested subspecies as they relate to geography. This is especially problematic if those assumptions are used to inform conservation or management decisions. However, increased awareness, documentation and scrutiny of measurable and reliable traits in field observation can lead to enhanced understanding of subspecies groups and inform their distributions.

ACKNOWLEDGEMENTS

We thank Olivia DaRugna for her assistance with field work and Nebraska Game and Parks District staff for assistance with accessing sites. All banding and handling of wild birds was conducted by trained personnel and approved under appropriate state and Federal bird banding permits.

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Recommended Citation

- Brenner, S.J. and J.G. Jorgensen. 2025. Clarifying Spotted Towhee subspecies in the Nebraska panhandle and the need for scientific studies on a phenotypic cline. Joint report of Audubon Great Plains and the Nebraska Game and Parks Commission, Gering and Lincoln, Nebraska, USA.