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Continuous, age-related plumage variation in male Kirtland's Warblers

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ABSTRACT. The ability to age individual birds visually in the field based on plumage variation could provide important demographic and biogeographical information. We describe an approach to infer ages from a distribution of plumage scores of free-ranging male Kirtland's Warblers (*Dendroica kirtlandii*). We assigned ages to males using a scoring scheme (0–12 points) based on variation in plumage coloration, brightness, and contrast on three dorsal and three ventral body regions presumed to be age-related. The distribution of total additive plumage scores for 875 breeding males was normally distributed, indicating no distinct age classes. Thus, we developed provisional plumage-age classes of second year (SY) and after second-year (ASY), and compared them to the total plumage scores of a smaller subsample of known age ($N = 92$) and minimum age ($N = 143$) males. Plumage scores of known-age male Kirtland's Warblers increased nonlinearly with age ($r_s = 0.67$), but with some overlap. The median plumage score for SY males (median = 5.0) was significantly lower than for third-year (TY) males (median = 7.0) and after third-year (3 year and older) males (median = 8.0), indicating that the plumage of male Kirtland's Warblers becomes more distinctive and brighter with age. Linear discriminant function analysis differentiated ASY male Kirtland's Warbler from SY males with 78.3% accuracy. Investigators could use the distribution of plumage scores and approximate age structures to document changes in male age structure during colonization, use, and abandonment of habitats by Kirtland's Warblers or other species that occupy early successional habitats. Aging free-ranging birds based on a plumage scoring scheme may be especially critical for demographic studies of less-studied species where it is unlikely that a banding program will be initiated, but where plumage-age inferences or management decisions must be made.

SINOPSIS. **Variaciones continuas en el plumaje de machos de de *Dendroica kirtlandii* relacionadas a su edad**

Describimos una forma para inferir la edad a través de una distribución de marcadores en machos silvestres de la reinita *Dendroica kirtlandii*. Utilizando dicho acercamiento, asignamos edad relativa a machos basándonos en un esquema de puntuación (0–12) para la coloración del plumaje, su brillantez, y contraste en tres localidades del dorso y la parte ventral, que han sido relacionadas con la edad de estos. La distribución de las puntuaciones de 875 machos fue normal, lo que indica que no hubo forma de distinguir las diferentes edades. Por ende, desarrollamos un divisiones de clases, basándonos en diferencias en el plumaje para individuos de segundo año (SA) y posterior al segundo año (PSA) y los comparamos a las puntuaciones de una pequeña muestra de aves ($N = 92$) cuya edad era conocida y a otra en que sabíamos la edad mínima ($N = 143$). La puntuación total para individuos de edad conocida aumento de forma no-lineal con la edad (Rs = 0.67), con un pequeño solapamiento en el plumaje total. La puntuación para machos de segundo año (SA) (mediana = 5.0) fue significativamente menor que para aves de tercer año (mediana = 7.0) y esta a su vez que para aves mayores a tres años (mediana = 8.0), lo que indica que el plumaje de los machos, en las aves estudiadas, se torna más brillante con la edad. Un análisis lineal de función discriminativa pudo diferenciar entre aves PSA y SA con un 78.3% de exactitud. Los investigadores han utilizado estas diferencias en el plumaje para clasificar entre los grupos machos territoriales que no han sido anillados. También pudieran utilizar estas particularidades y diferencias en el plumaje para aproximar la estructura de edades entre machos silvestres y hacer inferencias sobre la demografía y reclutamiento de aves en habitats de diferente calidad.

Key words: *Dendroica kirtlandii*, Kirtland's Warbler, molt, plumage-age classification, plumage variation

Plumage differences among male passerines have evolutionary and ecological implications (Rohwer et al. 1980, Procter-Gray and Holmes 1981). For example, second-year (SY) males may arrive later in the spring or settle in less-suitable territories (Ficken and Ficken 1967, Lanyon and Thompson 1986, Marra et al. 1998), have less site tenacity (Zimmerman 1982), and obtain mates less often than older males (Ficken and Ficken 1967, Carey and Nolan 1979, Hill 1988, Lanyon and Thompson 1986). Thus, distinguishing SY from after second-year (ASY) male

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birds may be important in studies of demography and recruitment for species using habitats that differ in quality.

Many passerine males do not achieve their definitive alternate plumage until their third calendar year (TY) due to fewer or duller alternate feathers (Pyle 1997). Males of some species have an obvious, discontinuous difference in color or color intensity (delayed plumage maturation) between SY males (i.e., males in their first alternate plumage) and older individuals. Other species have differing degrees of feather brightness and less distinguishable SY males (continuous plumage maturation), or simply attain full plumage maturation after their first prealternate molt (Rohwer et al. 1980).

Although inferring age based on plumage variation may be especially applicable to free-ranging passerines where a large sample of known-age individuals is not available or feasible to obtain (Graves 1997), it has rarely been attempted. The ability to age males visually in the field based on plumage variation could provide important demographic and biogeographical information on large samples of passerine birds over larger areas. Specifically, the ability to age male Kirtland's Warblers (*Dendroica kirtlandii)* in the field would facilitate studies of dispersal, colonization, annual recruitment, and habitat quality and turnover (Probst 1986, 1988, Probst and Weinrich 1993, Probst et al. 2003).

Previous investigators believed that SY male Kirtland's Warblers could be recognized by streaking or spots on the breast, and poorly defined black lores (Van Tyne 1953, Mayfield 1960, Goodman 1982, Walkinshaw 1983). However, the proportion of males with these characteristics is smaller than would be consistent (Mayfield 1953, Probst, pers. obs.) with estimates of 30–40% adult mortality (Bart et al. 1999). Using breast spots alone as an age criterion, Goodman (1982) found no differences between presumed older males without breast spots and presumed SY males with breast spots, except for wing length, suggesting that breast spotting may not be a reliable criterion for age classification. Although no previous delineations using multiple ageing criteria have been attempted between SY males and older age classes, we noticed other plumage characteristics of males that suggested less complete prealternate molting or differences in color intensity of alternate feathers that might provide better criteria for separating SY males from older males. However, these characteristics may not co-occur, so consistent and distinct age criteria are complicated for many species (Pyle 1997).

The objectives of our study were to describe age-related plumage variation in male Kirtland's Warblers using multiple plumage characteristics and to test a scoring scheme for aging free-ranging male Kirtland's Warblers in alternate plumage during the breeding season without capturing birds. Because of the difficulty of obtaining large, unbiased samples of known-age birds for many less-studied species, our approach was to first infer male plumage-age relations from a sample of male Kirtland's Warblers and then test those inferences with a smaller subsample of known-aged males. Our objective was to determine whether age-categories derived from plumage characteristics of a large, representative sample provided a reasonable estimate of age by comparing the assigned plumage score to a smaller, perhaps less representative subsample of known-age, banded males.

METHODS

We observed singing male Kirtland's Warblers from mid-May to mid-July after the prealternate molt in six counties in the Lower Peninsula of Michigan and three counties in the Upper Peninsula of Michigan. We devised a plumage-scoring scheme based on JRP's 7 years of experience observing the full range of plumage variation of free-ranging males prior to this study. Based on body regions that varied in color and brightness, the scoring scheme involved assigning scores to six body regions (three dorsal and three ventral) of male Kirtland's Warblers (Table 1). We recognize some subjectivity in assigning scores to free-ranging birds, but age classes within a species are not as distinct as differences among species (Pyle 1997). Because some plumage characteristics of SY males may overlap those of females, identifying SY males was sometimes difficult. In such cases, the best criteria for sex discrimination were a male's song and mask (lores). Almost all singing SY males observed had an identifiable mask, and females rarely did. For each body region, plumage scores were assigned from 0.0 to 2.0 (±0.25). As a result, the maximum total score for a male was 12. To eliminate interobserver bias, only JRP assigned scores to the plumage of

Table 1. Description of plumage characteristics used to score individual male Kirtland's Warblers. Numbers in parenthesis indicate the corresponding numerical value for that plumage interval.

Body region	Brighter (2.0 ≥1.0)	Unclassifiable (1.0)	Duller (<1.0–0.0)
DORSAL			
Mask	Thick, distinct black band	Thin, missing feathers	Vague or absent
Head	Blue or blue-gray (dark)	Light blue/dark gray or blue front (crown), brown posterior (nape)	Gray and/or yellow-brown posterior
Back	Dark black stripes on blue back	Brown-black stripes on yellow-brown back	Brown stripes on brown back (low contrast)
VENTRAL			
Throat	Bright, intense solid yellow	Light, faded yellow	Cream yellow or white
Breast	Bright, solid yellow	Light faded yellow; small brown/black specks on yellow	White, mottled appearance; large specks on cream yellow or white
Abdomen	Solid yellow	Light, faded yellow	Buff or white

free-ranging male Kirtland's Warblers ($N=875$) observed in the field from 1984 to 2001.

Because our unknown-age sample was obtained over more years, locations, regeneration types, and stand ages, it should be more representative of the full range of ages and plumages than the known-age subsample. Therefore, we examined the distribution of scores from the 875 male scores to provide a context for evaluating the distribution of scores of the smaller known-age sample. Otherwise, a sample of known-age birds not representative of the population might result in age categories defined at inappropriate points.

Of 875 males, we knew the age of 65 banded in the fall of their hatch year (HY; hereafter referred to as known-age males). Because the plumage of some of these males was subsequently scored in multiple years, we had a subsample of 92 known-age males. We compared the classification results from these known-aged males to a subsample of ASY males ($N = 143$) banded in the spring or late summer. Thus, we can only ascertain the minimum age of these ASY males instead of their exact age. We eliminated males with a minimum age of SY to create a subsample of 94 ASY males (≥3 calendar years) out of 143 AHY banded males. We assumed these plumage scorings were unbiased because males were banded by other investigators. Scores for the same bird among years were assumed to be independent because JRP did not have records of previous scores when in the field.

Male age was based on calendar years (2nd= SY, 3rd = TY, and ≥ 3 = after third year [ATY]) for comparing median scores of known-age birds. We combined older birds (≥3 years) into a single age class due to small sample sizes, and combined TY males in their third calendar year with older ASY males for purposes of classification-error determination and linear discriminant function (LDF) analysis of SY versus ASY males. We determined the percent error in determining the age of a male based on plumage score by comparing the assigned total plumage score for this subsample of banded males to their actual age class. We predicted that the classification error would consist primarily of males with intermediate plumage scores, and that a disproportionate number of these intermediate males would be in the TY subset of ASY males and would confound consistent discrimination of TY and ATY males as a combined ASY category from SY males. We did not attempt to discriminate TY males from older or younger males, but used proportions of TY males to help explain misclassifications.

Because scores of known-aged males could not be normalized by transformation, a Spearman rank correlation was used to examine the relationship between plumage score and age. A Kruskal-Wallis ANOVA was used to determine if total plumage-age scores differed among males of known ages (i.e., calendar years). All analyses were conducted using the Statistical Analysis System (SAS Institute 2000).

To determine the relation between the six body regions and the age classes (i.e., SY vs. ASY males) of the 65 known-age males, we used LDF analysis. A discriminant function analysis finds linear combinations of the original variables using a weighted sum of values on predictor variables (i.e., individual body region scores) that maximizes differences among age groups (Manly 1986). We used cross-validation to reduce bias in the original model. The variance–covariance matrix was used to derive the discriminant function. For males scored in multiple years, only the oldest score was included in the discriminant function analysis to increase observations in the older ages. Males were classified as either SY ($N = 35$) or ASY (at least 2–5 breeding seasons; $N = 30$). The LDF was also applied to the subsample of 94 AHY males to determine the classification error for ATY males in at least their second breeding season. Individual male Kirtland's Warblers of unknown age may be classified by the resulting linear function when plumage scores of the body regions are assigned to them.

RESULTS

Plumage variation and age. The distribution of plumage scores showed a discontinuity at the 6.0–6.9 score interval (Fig. 1A). We designated males in this plumage-score range (13.4%) as unclassified due to uncertainty whether they

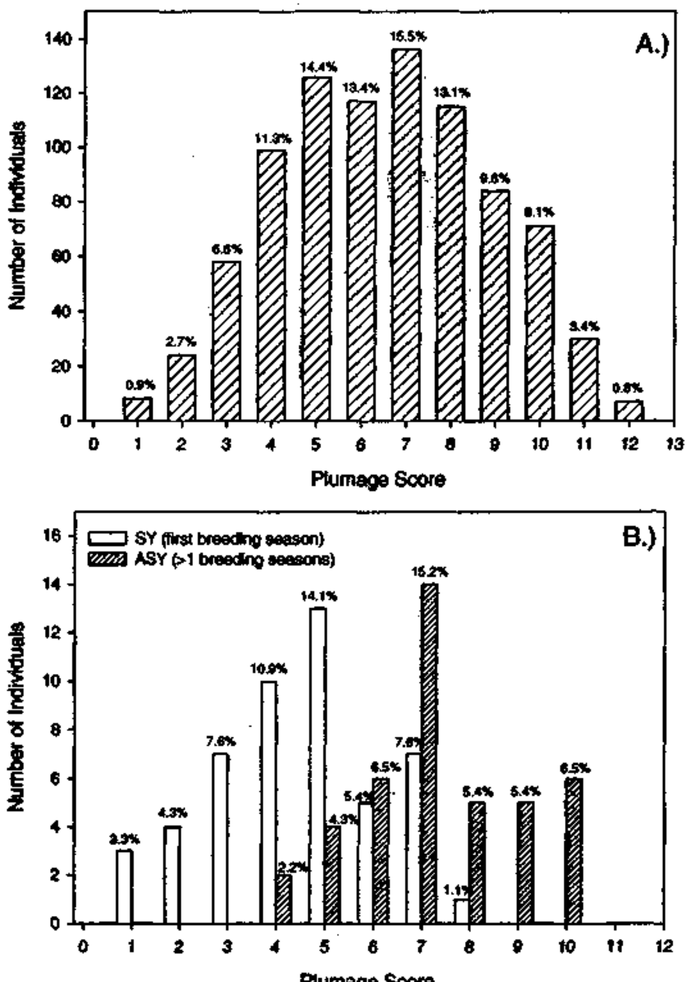

Fig. 1. Distribution of plumage scores assigned to male Kirtland's Warblers during the breeding season: (A) Plumage score distribution of 875 males showing continuous distribution of scores, and (B) score distribution of known-age male Kirtland's Warblers ($N = 92$) showing bimodality of scores.

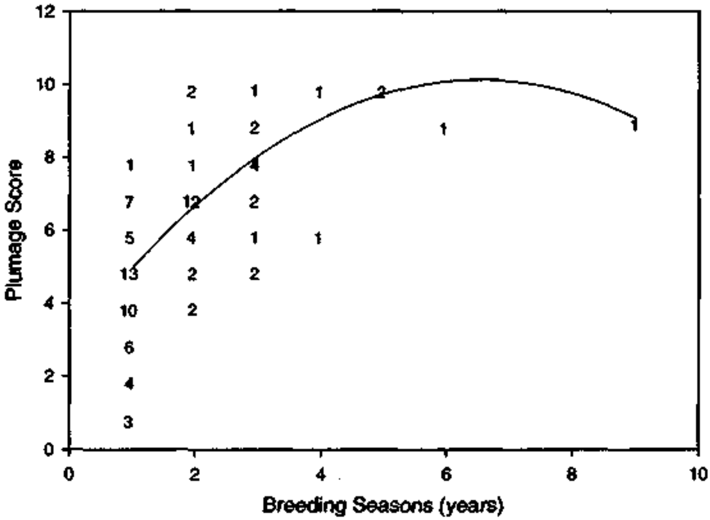

Fig. 2. Relation between total plumage score based on six body regions and age of known-age male Kirtland's Warblers ($N = 92$) scored during the breeding season in northern Michigan. Numbers represent the frequency of observations. There was a significant quadratic relationship between plumage score and age of males ($F_{2,89} = 33.7$, $P = 0.0001$).

were SY, TY, or ATY males. Males with plumage scores ≥ 7.0 were assumed to be in definitive alternate plumage and in at least their third calendar year (ASY male). Thus, the distribution of these observed plumage scores (e.g., Mountjoy and Robertson 1988) was used to infer the following plumage-age classes: SY (plumage score <6.0), unclassified (plumage score 6.0–6.9), and ASY (plumage score ≥ 7.0).

The distribution of plumage scores for known-age males indicated that age could potentially be discriminated as either SY or ASY at first approximation, based on the overlapping, bimodal distribution of plumage characteristics of known-age males (Fig. 1B). For known-age male Kirtland's Warblers, 54% were assigned plumage scores during their second year (SY), 26% in their third year (TY), and 20% in their third or later breeding seasons (ATY). Total plumage scores increased with age ($r_s = 0.67$, Fig. 2) as did total dorsal and total ventral scores ($r_s =$ 0.62 and 0.52, respectively), but total plumage scores of SY and ASY males overlapped (Fig. 1B). Total plumage scores varied significantly by age class ($F_{2,89} = 31.9$, $P \leq 0.01$). The median total plumage score for SY males (median = 5.0) was significantly lower than for TY males (median = 7.0) and ATY males (median = 8.0), indicating that male plumage becomes more distinctive and brighter with age.

Except for the throat, individual body regions had scores ranging from 0.0 to 2.0 (Fig. 3). The range for the throat was narrower (0.5 – 2.0). Most correlations among body regions were positive, but low (r_s <0.50), with the strongest correlation between the mask and head regions ($r_s = 0.61$; Table 2). Scores for the abdomen region had no correlation with the throat and back regions, and the mask, head, and throat areas tended to have higher scores than other body areas. The abdomen area score was less variable and generally scored about 1.0 (Fig. 3).

Discrimination and classificiation. On the basis of the total plumage scores of known-age birds ($N = 92$), the ages of 16.7% and 17.8% of ASY and SY males, respectively, were misclassified. Six of 36 ASY males were misclassified as SY (two males scored 4, and four scored 5), and 8 of 45 SY males were classified as ASY (seven males scored 7, and one scored 8; Fig. 1b). Eleven males (11.9%) were unclassified (plumage score = 6.0– 6.9), including 5 SY males, 4 TY males, and 2 ATY males.

For the subsample of ASY males, 8 of 94 were incorrectly scored as first-year males (plumage

Table 3. The number (percent) of male Kirtland's Warblers classified as ASY and SY males based on linear discriminant function analysis using plumage scores of 65 males. Results represent cross-validated classification rates.

	Number allocations to group		
Source group	ASY	SY	Total
Adult males	**28 (80)**	7 (20)	35 (100)
First-year males	7 (23)	**23 (77)**	30 (100)
Total	35 (54)	30 (46)	**65 (100)**
Priors	0.5	0.5	

have a distinct SY subadult plumage. Higher plumage scores were associated with more intense color and contrasting plumage, indicating that most males attain definitive alternate plumage by their second breeding season in their third calendar year.

Our results indicate that SY males are typically duller than ASY males in alternate plumage. Most male Kirtland's Warblers with plumage scores between 6 and 6.9 were SY and TY males. The largest error in classifying ASY males was for those in their third calendar year displaying intermediate-plumage characteristics. The reduced error in classifying the subsample of ASY males in at least their second spring also suggests that errors in identifying ASY males were largely limited to TY males. These results help explain the continuous, age-related plumage pattern for all males because TY males may represent a disproportionate number of intermediate scores. However, the known-age subset (Fig. 1B) of the 875 total males scored (Fig. 1A) shows that the known-age subsample was not representative of the larger population. Specifically, the known-age subsample had relatively more low-scoring males and fewer high-scoring males, indicating a bias toward SY males in the known-age subsample. A potential reason for this bias may be due to a disproportionate number of HY males banded during the summer relative to AHYs. In addition, most known-age males were scored in the year after banding, and only 8 of 92 were scored four or more years after banding.

Male Kirtland's Warblers with higher total plumage scores often retained low scores for one or more characteristics. For example, many breeding males more than 3 years old retained light speckling on the breast, contradicting the past age determination criterion of Goodman (1982). The relatively low mean scores for the back and breast areas show that many male Kirtland's Warblers retain brownish stripes on a gray–brown or brown back and speckling on their breasts into their second and third calendar years. The latter contrast may be related to some body areas retaining more in the basic (head, mask, throat, and breast) versus alternate feathers (abdomen and back; C. Bocetti, pers. comm.) or having more duller alternate feathers in some areas than others (Pyle 1997). Nevertheless, although some scores were more variable than others, inclusion of all six body regions permitted better discrimination of age classes. For example, after several years of scoring male Kirtland's Warbler plumages, we noticed that many presumed SY males had rusty rather than brown primary feathers, a characteristic typical of older male *Dendroica* warblers (P. Pyle, pers. comm.) This

Table 4. Linear discriminant functions for discriminating ASY from SY male Kirtland's Warblers ($N = 65$) during the breeding season using plumage scores of six body regions.

Plumage color characteristic	Coefficient			Structure coefficient
	SY	ASY	Difference	
Mask	1.66	2.15	−0.49	0.71
Head	2.88	5.19	−2.31	0.91
Back	−0.36	0.40	−0.76	0.69
Throat	8.73	10.03	−1.31	0.56
Breast	−3.00	−2.02	−0.98	0.68
Abdomen	6.30	6.17	0.13	0.26

fits the pattern of annual molting because AHY males molt their primaries in the prebasic molt, whereas immature (HY) males retain juvenal primaries (Pyle 1997). Thus, we suggest adding this characteristic in future applications for aging *Dendroica* warblers.

Some classification errors will always occur when separating individuals within species because of variability in plumage and molting patterns (Pyle 1997). Error rates in aging male Kirtland's Warblers in our study were high enough to preclude reliable (e.g., 95% accuracy) aging of all males, and this may or may not be acceptable depending on how the scores are used. For example, plumage variability without individual age determination, plus territoriality and song variability, has been used to help distinguish males from neighbors in a breeding area, but not from males in other areas (Probst et al. 2005). In addition, the relative numbers of SY and ASY males in habitats of different quality may allow inferences about the age distribution of males among habitat types and the demographic consequences on populations (Zimmerman 1982, Lanyon and Thompson 1986, Probst 1988).

In addition, the distribution of plumage scores or an approximate age structure could be used to document changes in male age structure during colonization, use, and abandonment of habitats by Kirtland's Warblers or other species that occupy early successional habitats. This is important because changes in Kirtland's Warbler populations have been related to compensatory effects of colonization of young stands and maturation of those too old to support breeding pairs (Probst 1986). Determining the approximate age of free-ranging males based on plumage variation can help identify patterns of colonization by ASY and SY males without costly banding programs. For example, we may be able to estimate the approximate age of Kirtland's Warblers relative to the age of jack pine stands where they breed, even if some males remain unclassified. Such general, but less precise, models are vital for ecological applications, especially when detailed study is neither possible nor timely (Johnson et al. 1999).

Aging free-ranging birds based on a plumage scoring scheme may be especially critical for demographic studies of less-studied species where it is unlikely that a banding program will be initiated, but where plumage-age inferences or management decisions must be made. The age structure of a population can be estimated locally or can be used to compare age structure among localities without determining the age of any one individual, facilitating inferences about age structure in time and space. However, we reiterate that "age-class data for free-living birds should only be collected by investigators with extensive experience ... with the natural range of age-related plumage variation in the focal species" (Graves 1997).

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