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Ornithological Methods

Quantification of physiological aging criteria utilizing window strike data

Cuantificación de criterios fisiológicos de envejecimiento utilizando datos de impactos contra ventanas

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ABSTRACT. Recent studies have been interested in the effects of age on window strike vulnerability in avian species. To accurately assess age-dependent patterns in avian populations, proper aging criteria should be used to allow for comparisons across studies. Recent window strike studies rely heavily on skull ossification, and we were interested in the accuracy of this method compared to other physiological-based age determinations in passerines and non-passerine landbirds. In this study, we quantitatively analyzed three potential aging criteria that can be used for aging specimens: presence/absence of the bursa of Fabricius, skull ossification, and gonadal maturity. To our knowledge, this is the first quantitative comparison of these criteria. While one study did qualitatively compare the number of agreements versus disagreements between these methods, our study expands on this research by implementing a statistical approach. Skull, bursa, and gonad measurements all were significantly and positively correlated with each other. Nevertheless, we did find disagreement between the methods when further exploring their relationships using Generalized Linear Models. For example, when we compared the number of adult females with immature females to test for window strike vulnerability using a Chi-square test, all three aging criteria produced similar results. Adult females showed a statistically higher rate of window strikes than immature females. However, we still suggest caution using only one criterion to age specimens. In summary, while we did find these three aging characters to be highly correlated, disagreement does exist between these characters.

RESUMEN. Estudios recientes se han interesado por los efectos de la edad en la vulnerabilidad a los golpes contra ventanas en especies de aves. Para evaluar con precisión los patrones dependientes de la edad en las poblaciones de aves, deben utilizarse criterios de envejecimiento adecuados que permitan realizar comparaciones entre los distintos estudios. Los estudios recientes sobre el impacto contra ventanas se basan en gran medida en la osificación del cráneo, y nos interesaba conocer la precisión de este método en comparación con otras determinaciones fisiológicas de la edad en aves terrestres Passeriformes y no Passeriformes. En este estudio analizamos cuantitativamente tres posibles criterios de envejecimiento que pueden utilizarse para determinar la edad de los especímenes: presencia/ausencia de la bursa de Fabricio, osificación del cráneo y madurez gonadal. Hasta donde sabemos, ésta es la primera comparación cuantitativa de estos criterios. Si bien un estudio comparó cualitativamente el número de acuerdos frente a desacuerdos entre estos métodos, nuestro estudio amplía esta investigación mediante la aplicación de un enfoque estadístico. Las mediciones del cráneo, la bursa y las gónadas mostraron una correlación significativa y positiva entre sí. No obstante, encontramos discrepancias entre los métodos al explorar más a fondo sus relaciones mediante modelos lineales generalizados. Por ejemplo, cuando comparamos el número de hembras adultas con el de hembras inmaduras para comprobar la vulnerabilidad a los golpes contra ventanas mediante una prueba de Chi-cuadrado, los tres criterios de envejecimiento arrojaron resultados similares. Las hembras adultas mostraron una tasa estadísticamente más alta de golpes contra ventanas que las hembras inmaduras. Sin embargo, seguimos sugiriendo precaución a la hora de utilizar un solo criterio para determinar la edad de los especímenes. En resumen, aunque encontramos que estos tres caracteres de envejecimiento están altamente correlacionados, existe desacuerdo entre ellos.

Key Words: *bursa of Fabricius; gonads; skull ossification; specimens; window strikes, aging*

INTRODUCTION

Bird specimens are an excellent resource to ornithologists; nevertheless, determining the age of specimens can prove difficult if solely relying on plumage characters alone. Numerous studies use bird specimens for research, including window strike studies. Window strikes are the second largest anthropogenic cause of bird deaths in North America (Klem 1989, Loss et al. 2014), and current studies estimate window strikes to cause between 100 million to 1 billion avian deaths in the United States annually (Klem Jr 1990, Loss et al. 2014). Of these studies, a select few have examined the role of age with window strikes and have shown age-dependent patterns, with immature birds experiencing higher mortality rates than adults (Hager and Craig 2014, Loss et al. 2014, Kahle et al. 2016). Understanding how age correlates with window strikes is crucial for conservation managers to understand how it affects avian populations. However, no guidelines on best practices for aging prepared specimens or recently deceased birds exist to our knowledge beyond Pyle (1997), and the aging methods used across previous studies are variable. This inconsistency in aging could impact the interpretation of results and make it difficult to extrapolate patterns from data across studies. In this study, we look at the amount of statistical agreement between three methods of aging specimens: skull ossification, presence/absence of the bursa of Fabricius (henceforth referred to as bursa), and gonadal maturity. While the agreement of these three methods has been qualitatively compared (see Davis 1947), this study is the first to our knowledge to quantitatively analyze these aging characters in passerines and non-passerine landbirds.

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Skull ossification (also known as skull pneumatization) is a standard aging method used for avian specimens (Miller 1946, Davis 1947, McNeil and Burton 1972, Stewart 1972, Pyle 1997, 2008). It is common to assign the skull a percent estimate (between 0-100%) of ossified to unossified areas of the skull. Skull ossification describes ontogenesis of a bird's skull during its first calendar year of life (Pyle 1997). Skulls of recently fledged passerines and non-passerine landbirds consist of only one layer of bone. As the bird progresses into its first year, a second layer begins to develop forming spaces (air pockets) in the skull. These two layers of bone are joined by columns, a process coined skull ossification (Miller 1946, Niethammer 1968, McNeil and Burton 1972, Stewart 1972, Pyle 1997). When using Pyle (1997), all North American birds are said to be Hatching-Year (HY) from hatching to December 31st, and thereafter After-Hatching-Year (AHY) (Pyle 1997). Depending on time of year, the latter category in many cases has fully developed skulls although non-passerine landbirds skulls have been reported to never fully ossify (Pyle 1997, 2008). While ossification has been assessed in numerous songbird species (Chapin 1949, Leberman 1970, Stewart 1972, Hamel and Beacham 1983, Wiley and Piper 1992), it has not been quantitatively assessed in conjunction with the bursa or gonadal maturity in passerines and non-passerine landbirds.

The second method of aging birds that has received limited consideration is the presence/absence of the bursa of Fabricius, a key development organ located above the dorsal wall of the cloaca (Davis 1947, Glick 1956, 1960, 1970; Pyle 2008). The bursa of Fabricius is found primarily in immature birds (Linduska 1943; Davis 1947, Glick 1956, 1983, McNeil and Burton 1972) although in some taxonomic groups, it never regresses and therefore is not a reliable age character in these cases (Taibel 1935, Glick 1960). The bursa is associated with sexual maturity and development (Glick 1956, 1960) and is the location of B-cell, or 'bursal-derived' cell, production. Glick (1956, Glick et al. 1956) discovered an inverse, negative relationship between the testes and adrenal glands with the bursa by injecting different breeds of Red Junglefowl (*Gallus gallus*) and ducks with androgens and corticosteroids. It was observed that in direct response to the injections, the bursa began pre-mature involution (Glick 1956, Glick et al. 1956). The discovery of this was significant because the bursa was previously thought to only regress after a bird reached sexual maturity and was not congruent to gonadal maturity (Jolly 1913, Glick 1956, Glick et al. 1956). Based on the experimental evidence, we would expect that a bird with a bursa would have immature gonads. We set out to test the amount of agreement between the bursa, gonads, and skull ossification.

METHODS

Data collection

We obtained 1,164 curated museum records of 110 different species, consisting of both passerines and non-passerine landbirds, from four institutions (Louisiana State University, University of Florida, Mississippi Museum of Natural History, and the University of Georgia) with window strike mortality listed as their cause of death (Table A1.1). Information collected from each specimen included strike location, date of strike, sex, age assigned, gonadal characters, bursa presence/absence, and percentage of skull ossification. Records spanned all months of the year.

Bursa information was recorded as either present or absent as noted by the data associated with the specimen as well as percent ossification of the skull (0-100%). Since specimen data did not have a distinction between mature and immature gonads, we developed standardized criteria for assigning maturity of female gonads based on the information in the database. We were only interested in the determination of mature versus immature gonads based on the morphology and appearance of the internal gonadal structures. Males are characterized by having gonadal symmetry with two testes whereas females have one ovary typically found on the left side exhibiting asymmetry (Guioli et al. 2014). While the gonads begin forming during development, they do not reach full maturity until sometime after fledging, and age at sexual maturity is variable across species (De Magalhães and Costa 2009, Guioli et al. 2014, Herculano-Houzel 2019). We classified female gonads as mature if the ovary contained at least one ovum or if the oviduct was wide and/or convoluted (as opposed to smooth or straight), indicating a prior breeding event. We did not include male gonads in this analysis due to the inability to discern age in testes.

Statistical analyses

We dummy coded the data to where a 100% ossification of the skull was coded as a mature bird (= 1), whereas incomplete ossification (<100%) was coded as immature (= 0). Similarly, the absence of a bursa (= 1) was considered a mature bird and the presence (= 0) as an immature bird. Lastly, fully developed female gonads were coded as mature (= 1) and gonads not fully developed (= 0) indicated an immature bird. We used the Generalized Linear Model (GLM) function of the lme4 package in R to test the agreement between the three aging criteria (Bates et al. 2014, R Core Team 2022). We also included sex as an explanatory variable in two of the GLM models to test for sex-specific effects on skull ossification and presence/absence of the bursa. We did not look for sex-specific effects in gonads since we did not have that information for males. We were unable to add the processor identification as a random variable as this information was lacking for most of the data. We used all the dummy coded data for the GLM models except we kept the percent ossification as a percentage and analyzed it as a numeric variable in the GLM models.

We used a Pearson Correlation to test for the agreement of age classification between skull ossification, presence/absence of the bursa, and gonadal maturity to calculate Pearson's Correlation Coefficient (r) for all three variables (bursa-gonad, bursa-skull, skull-gonad) (R Core Team 2022) using the dummy-coded data. To test how well these models performed, we also calculated the coefficient of determinations (R^2) for all three comparisons using the Linear Model function in R (R Core Team 2022). Additionally, we conducted Chi-square tests to look at patterns with age in females using all three aging criteria (R Core Team 2022). For these tests, we used an expected ratio of three immatures to one adult used by Klem (1989) which was derived from Lack (1954) and Peterson (1963).

RESULTS

Quantification of aging criteria

Skull, bursa, and gonad measurements all showed statistically significant positive correlations with each other (Table 1) (*p*-

Table 1. Pearson correlations (r), p-values, and Coefficient of determinations (R2) between skull, bursa, and gonadal measures of maturity.

	Pearson correlation (r)		Confidence Interval		Coefficient of determination (R^2)		Std. Error	
	Skull	Bursa	Skull	Bursa	Skull	Bursa	Skull	Bursa
Bursa	0.681 (<0.001)		(0.631 - 0.725)		0.464		(0.043)	
Gonads	0.625 (<0.001)	0.706 (< 0.001)	(0.507 - 0.720)	(0.608 -0 .783)	0.390	0.499	(0.085)	(0.064)

values = < 0.001). These positive values between bursa-skull, bursa-gonad, and skull-gonad correlations indicated agreement on estimates of maturity. The proportion of variance for the dependent variable that is explained by the independent variable (R^2) was determined between bursa-skull, bursa-gonad, and skull-gonad. The R^2 values from highest to lowest were 1) bursa-gonad at 50%, 2) bursa-skull at 46%, and 3) skull-gonad at 39%. To further explore these relationships, we used Generalized Linear Models (Bates et al. 2014). When we tested for the effect of sex on ossification we found for every 1% increase in ossification, the likelihood of a specimen being identified as a male over female increased by 1.5% (1.07-2.10; 95% C.L.) ($p = 0.02$). When we tested for the effect of gonads (mature or immature gonads as a proxy for age) on percent ossification, for every 1% increase in ossification, we found that a specimen was 12.3% more likely to be aged as mature over immature using gonads (5.28-31.32; 95% C.L.) ($p < 0.001$). When we tested for the effect of presence/absence of bursa on gonads, specimens with immature gonads were 38.3% more likely to be assigned to having no bursa over bursa (14.49-118.19; 95% C.L.) ($p < 0.001$). When we tested for the effect of bursa on percent ossification, we found for every 1% increase in ossification, we found that the specimen was 23.8% more likely to be assigned with no bursa (13.77-43.48; 95% C.L.) ($p < 0.001$). When we tested for the effect of sex on presence/absence of bursa, specimens with bursas were 2% more likely to be identified as male over female (1.45-2.86; 95% C.L.) ($p < 0.001$).

Age patterns with females

We used Chi-square tests to look at patterns between immature and adult female birds in our dataset using the same three aging criteria. Our purpose in doing so was to test whether using different aging criteria would impact the overall results. We found a statistically significant difference between immature and adult females in the window strike dataset when using gonads as the aging criteria where adult female strikes are higher in the dataset than immatures (Fig. 1) (p-value < 0.001; $X^2 = 84.933$). We found a similar result when using bursa as the aging criteria (Fig. 2) (p-value < 0.001; $X^2 = 52.718$) as well as when using ossification (Fig. 3) (p-value < 0.001; $X^2 = 56.728$).

Fig. 1. Results from the Chi-square test using gonads as the determinate of age. Y-axis is the proportion of window strikes and the X-axis is the observed and expected values for both female adults and juveniles.

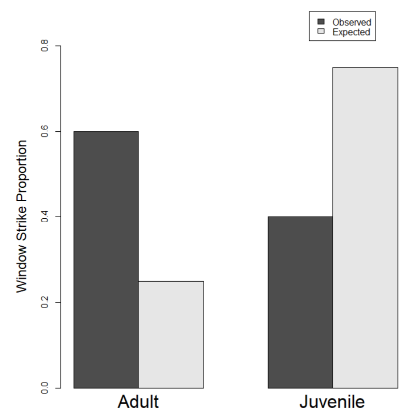
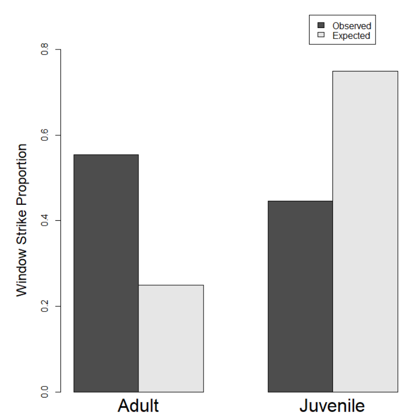


Fig. 2. Results from the Chi-square test using bursa as the determinate of age. Y-axis is the proportion of window strikes and the X-axis is the observed and expected values for both female adults and juveniles.



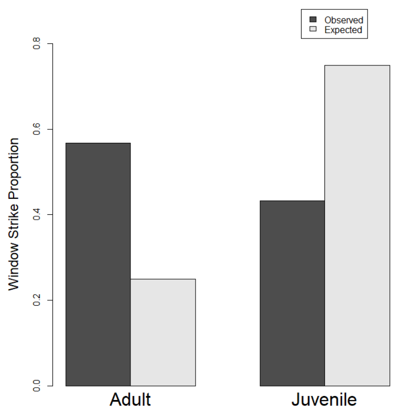
DISCUSSION

Aging criteria

In this study, we found that all three aging criteria, bursa, skull, and gonads, were positively correlated with one another (p-values = < 0.001). The relationship between gonads and the bursa performed the best with an R^2 of 50% and an r value of 71%.

However, when we explored this relationship further, there were a few disagreements where some records had no bursas but immature gonads (n = 7 out of 71 records)(Table A1.2). Davis

Fig. 3. Results from the Chi-square test using ossification as the determinate of age. Y-axis is the proportion of window strikes and the X-axis is the observed and expected values for both female adults and juveniles.



(1947) classified birds with bursas that had mature gonads, also showing disagreement between these two criteria. Additionally, the dataset included some birds with bursas, fully ossified skulls, and mature gonads. Interestingly, Davis did not report female birds with no bursas and immature gonads. Because Davis (1947) does report the numbers of males and females in the study, more study is needed to determine whether there is a sex-specific difference in the relationship between the gonads and the bursa. Furthermore, Davis (1947) did not report how immature versus mature gonads were determined, and we were unable to differentiate between mature and immature male gonads in our dataset. Future research should focus on whether bursal involution and gonadal maturity are congruous in passerines and non-passerine landbirds for males.

The bursa

The bursa is by far an understudied organ in wild songbirds. Studies have determined development and degeneration timing of the bursa in different breeds of Red Junglefowl (*Gallus gallus*) (Glick 1956, Glick et al. 1956), but there is limited information available on bursal involution in relation to developmental age in wild songbirds (Pyle 2008). While our study elucidated the relationship between the bursa presence/absence with other characteristics such as skull ossification, gonadal maturity, and sex, much work is needed to fully understand its role in wild songbirds. The bursa-gonad relationship had an R^2 value of 50%, meaning the two values are positively correlated, but we found that specimens assigned with immature gonads were 38% more likely to be assigned with no bursa when using a Generalized Linear Model. One possible explanation for this disagreement could be females with fully mature gonads were collected prior to the onset of their first breeding effort and thus would not have a convoluted oviduct, an ovum, or presence of prior breeding events. Additionally, it could be explained by processor error and the inability to locate the bursa. To further investigate this, we were interested in the effect that sex may have on bursa assignment. Specimens with bursas were 2% more likely to be identified as male over female (1.45-2.86; 95% C.L.) ($p < 0.001$). This could be an indication of sex-specific variation in timing of bursa involution of males versus females.

Using skull ossification

Several published studies rely heavily on skull ossification to classify age; some of these use a combination of criteria while others solely used skull ossification to determine age (Kessel 1951, Klem 1989, Hager and Craig 2014, Kahle et al. 2016, Colling et al. 2022). Our analysis revealed that there appears to be some sex variation in the timing of skull ossification. Thus, we advise caution on using this sole criterion based on our results and suggest using an additional criterion to confirm age. Previous research has revealed that the rate of skull ossification is species-dependent (Kessel 1951, Nero 1951, Grant 1966, Leberman 1970, McNeil and Burton 1972, Stewart 1972, Eaton 2001), but we suggest that other variables (such as environmental stressors) could also affect the rate of pneumatization in individuals. We do recognize that our data included records from throughout the calendar year and that most passerines cannot be reliably aged into their second calendar year (Pyle 1997). Since our aging analyses did include ten individuals classified as non-passerine landbirds, we examined these individually to determine if they would have more disagreements with ossification versus gonads and bursa since it has been reported that sometimes their skulls do not fully ossify (Pyle 1997). Of these, only four had disagreements between the bursa and ossification and only one disagreement between the gonads and the skull, thus, not affecting our results overall. Of note, 8 of the 10 individuals were reported as having 100% ossification. Nevertheless, we did find that all three aging criteria produced the same results overall (Fig. 1-3).

Plumage and molt characters

Curated specimens are an important resource for research but there are some limitations with what data specimens can provide such as age based on plumage and molt. Once a specimen has been prepared, it can be difficult without experience to determine age based on plumage and molt due to the inability to extend the wing out and because of natural color wear over time (Doucet and Hill 2009, Carrillo-Ortiz et al. 2021). Thus, we could not add age based on plumage and molt as an additional variable in our dataset. We suggest it would be helpful for avian specimen preparators to include specific molt and plumage information with the specimen records prior to preparation. Testing the agreement of age using molt and plumage in contrast with the three criteria we analyzed, may provide helpful insight into how to assess age more accurately. One reason this information may be excluded by museum curators could be because historically there was no standard method to record molt and plumage observations of a specimen when prepared. While the methods of Pyle (1997) allow researchers to assign an age, the molt and plumage observations are typically not transcribed on specimen labels. However, with the development of the three-letter plumage and molt system by Wolfe et al. (2012), this system could provide a solution (Wolfe et al. 2012, Pyle et al. 2022). Additionally, perhaps it is worth re-evaluating how we designate mature versus immature birds overall, especially when using terminologies found in Pyle (1997) where AHY is typically synonymous with a mature bird and an HY with an immature bird. Perhaps adding a physiological determinate of age alongside molt and plumage information will provide a more informative way to designate a mature or immature bird without using the cut-off date of December 31st to dictate age.

CONCLUSION

To our knowledge, this study is the first quantitative comparison of the bursa, skull, and gonads as aging criteria in passerines and non-passerine landbirds. We found that all three aging criteria were significantly correlated. Nevertheless, our results revealed some level of disagreement between the three aging criteria. Our study supported the findings of Davis (1947) who also found disagreements between these three aging criteria. Therefore, we recommend using more than one character when aging specimens. Finally, we emphasize the importance of avian specimens having detailed, complete records associated with them in museum collections. We suggest avian preparators and collections include date collected, location collected, cause of death, skull ossification, bursa, gonadal characters, and molt and plumage information whenever possible for future investigations into the accuracy of these aging criteria. While our Chi-square results revealed similar patterns with age and window strikes using all three criteria, using only one of these aging criteria could cause an overestimation or underestimation of a particular age group. Future studies should focus on how using molt and plumages as aging criteria correlates with skull ossification, the bursa, and gonadal maturity.

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Data Availability:

Data and code available upon reasonable request

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Appendix 1.

Supplementary Table 1**:** Species, common name, state collected, and totals of specimens used for the study.

SPECIES	COMMON NAME	AL	CA	FL	GA	LA	MS	NM	NC	TX	SPECIES TOTAL
Corvus brachyrhynchos	American Crow			1							**1**
Spinus tristis	American Goldfinch			9	2						**11**
Setophaga ruticilla	American Redstart			17			4				**21**
Turdus migratorius	American Robin			15	1	2		1			**19**
Peucaea aestivalis	Bachman's Sparrow			1							**1**
Icterus galbula	Baltimore Oriole			3							**3**
Hirundo rustica	Barn Swallow			1							**1**
Setophaga castanea	Bay-breasted Warbler			1							**1**
Mniotilta varia	Black-and-white Warbler			10			2				**12**
Coccyzus erythropthalmus	Black-billed Cuckoo				1						**1**
Setophaga fusca	Blackburnian Warbler			3							**3**
Setophaga striata	Blackpoll Warbler			2							**2**
Setophaga caerulescens	Black-throated Blue Warbler			13	1						**14**
Setophaga virens	Black-throated Green Warbler			2			1			2	**5**
Passerina caerulea	Blue Grosbeak			2							**2**
Cyanocitta cristata	Blue Jay			2							**2**
Polioptila caerulea	Blue-gray Gnatcatcher			1							**1**
Vireo solitarius	Blue-headed Vireo			3							**3**
Quiscalus major	Boat-tailed Grackle			2							**2**
Spizella breweri	Brewer's Sparrow							1			**1**
Certhia americana	Brown Creeper						1				**1**
Toxostoma rufum	Brown Thrasher			1		1	1			2	**5**
Molothrus ater	Brown-headed Cowbird						3				**3**
Cardellina canadensis	Canada Warbler			1			1		2		**4**
Setophaga tigrina	Cape May Warbler			4	1						**5**
Poecile carolinensis	Carolina Chickadee			1							**1**
Thryothorus ludovicianus	Carolina Wren			1							**1**
Petrochelidon fulva	Cave Swallow			1							**1**
Bombycilla cedrorum	Cedar Waxwing		2	47	2	63	5				**119**
Setophaga pensylvanica	Chestnut-sided Warbler			1							**1**

Chaetura pelagica	Chimney Swift		3							**3**
Spizella passerina	Chipping Sparrow		1							**1**
Antrostomus carolinensis	Chuck-will's-widow		1							**1**
Quiscalus quiscula	Common Grackle		2							**2**
Columbina passerina	Common Ground Dove		2							**2**
Chordeiles minor	Common Nighthawk		1							**1**
Geothlypis trichas	Common Yellowthroat		21		27	2			39	**89**
Oporornis agilis	Connecticut Warbler		2							**2**
Junco hyemalis	Dark-eyed Junco							1		**1**
Dryobates pubescens	Downy Woodpecker		5							**5**
Sialia sialis	Eastern Bluebird		3							**3**
Sayornis phoebe	Eastern Phoebe		1							**1**
Pipilo erythrophthalmus	Eastern Towhee		1							**1**
Streptopelia decaocto	Eurasian Collared-Dove		1							**1**
Sturnus vulgaris	European Starling		4							**4**
Coccothraustes vespertinus	Evening Grosbeak		2	3						**5**
Corvus ossifragus	Fish Crow		1							**1**
Passerella iliaca	Fox Sparrow			3						**3**
Regulus satrapa	Golden-crowned Kinglet					7				**7**
Ammodramus savannarum	Grasshopper Sparrow		2							**2**
Dumetella carolinensis	Gray Catbird		12	1	15	4			1	**33**
Tyrannus dominicensis	Gray Kingbird		1							**1**
Catharus minimus	Gray-cheeked Thrush		6			6				**12**
Myiarchus crinitus	Great Crested Flycatcher		4							**4**
Catharus guttatus	Hermit Thrush		4	3		9				**16**
Setophaga citrina	Hooded Warbler		5	2		2				**9**
Haemorphous mexicanus	House Finch		2							**2**
Passerina cyanea	Indigo Bunting		13	1	57				8	**79**
Geothlypis formosa	Kentucky Warbler		4			7				**11**
Lanius ludovicianus	Loggerhead Shrike		1							**1**
Parkesia motacilla	Louisiana Waterthrush		2			3				**5**
Geothlypis tolmiei	MacGillvray's Warbler	1								**1**
Setophaga magnolia	Magnolia Warbler		3		1	4			9	**17**
Cistothorus palustris	Marsh Wren		2							**2**
Zenaida macroura	Mourning Dove		11		4	1			1	**17**

Cardinalis cardinalis	Northern Cardinal		15	1	140	8	1	**165**
Colaptes auratus	Northern Flicker		3					**3**
Mimus polyglottos	Northern Mockingbird		1		3	2	1	**7**
Setophaga americana	Northern Parula		7			2		**9**
Parkesia noveboracensis	Northern Waterthrush		5			3		**8**
Icterus spurius	Orchard Oriole		1					**1**
Seiurus aurocapilla	Ovenbird	1	28		6	4	8	**47**
Passerina ciris	Painted Bunting		7			1		**8**
Setophaga palmarum	Palm Warbler		10					**10**
Dryocopus pileatus	Pileated Woodpecker		5					**5**
Spinus pinus	Pine Siskin		2	1				**3**
Setophaga pinus	Pine Warbler		1					**1**
Setophaga discolor	Prairie Warbler		1					**1**
Protonotaria citrea	Prothonotary Warbler		10		15	12	1	**38**
Haemorphous purpureus	Purple Finch		25	7				**32**
Melanerpes carolinus	Red-bellied Woodpecker		6					**6**
Vireo olivaceus	Red-eyed Vireo		13	1	1	2		**17**
Melanerpes erythrocephalus	Red-headed Woodpecker			1				**1**
Agelaius phoeniceus	Red-winged Blackbird		4					**4**
Pheucticus ludovicianus	Rose-breasted Grosbeak		8	1				**9**
Corthylio calendula	Ruby-crowned Kinglet					2		**2**
Archilochus colubris	Ruby-throated Hummingbird		7	2				**9**
Selasphorus rufus	Rufous Hummingbird		1					**1**
Passerculus sandwichensis	Savannah Sparrow		1					**1**
Piranga olivacea	Scarlet Tanager		2	2				**4**
Icterus pectoralis	Spot-breasted Oriole		2					**2**
Piranga rubra	Summer Tanager		8					**8**
Catharus ustulatus	Swainson's Thrush		15	1		8		**24**
Limnothlypis swainsonii	Swainson's Warbler		5					**5**
Melospiza georgiana	Swamp Sparrow		3					**3**
Leiothlypis peregrina	Tennessee Warbler		1	2		1		**4**
Tachycineta bicolor	Tree Swallow		1					**1**
Baeolophus bicolor	Tufted Titmouse		1			1		**2**
Catharus fuscescens	Veery		13			3		**16**
Vireo griseus	White-eyed Vireo		2		2	1		**5**
Zonotrichia albicollis	White-throated Sparrow		1					**1**

Hylocichla mustelina	Wood Thrush			10			15		1		**26**
Helmitheros vermivorum	Worm-eating Warbler			2			3				**5**
Setophaga petechia	Yellow Warbler			2			1				**3**
Sphyrapicus varius	Yellow-bellied Sapsucker			20	1						**21**
Coccyzus americanus	Yellow-billed Cuckoo			17	1		7				**25**
Icteria virens	Yellow-breasted Chat						1				**1**
Setophaga coronata	Yellow-rumped Warbler	1		10		9	3				**23**
Vireo flavifrons	Yellow-throated Vireo			3		1					**4**
Setophaga dominica	Yellow-throated Warbler			1							**1**
	State Totals	**2**	**3**	**548**	**42**	**347**	**143**	**2**	**4**	**73**	**1164**

Supplementary Table 2**:** Data used for the aging criteria analyses listing species, totals, and the number of agreements versus disagreements. *Note that the denominator is the total age categories (ossification, bursa, and gonads) available for those records since not all records had all three available. The numerator is the number of characters which agreed.

SPECIES	TOTAL	3/3	2/3	2/2	1/2
American Goldfinch	5	2	0	3	0
American Redstart	9	2	1	5	1
American Robin	3	2	0	1	0
Baltimore Oriole	1	0	0	1	0
Barn Swallow	1	1	0	0	0
Bay-Breasted Warbler	1	0	0	1	0
Black-and-white Warbler	4	2	0	1	1
Blackburnian Warbler	2	1	0	1	0
Black-throated Blue Warbler	6	0	0	6	0
Black-throated Green Warbler	1	0	0	1	0
Blue Jay	2	0	0	2	0
Blue-headed Vireo	1	0	0	1	0
Boat-tailed Grackle	1	0	0	1	0
Brewer's Sparrow	1	1	0	0	0
Brown Thrasher	4	2	0	2	0
Brown-headed Cowbird	1	0	0	1	0
Canada Warbler	2	1	0	1	0
Cape May Warbler	2	0	0	1	1
Carolina Wren	1	0	0	1	0
Cave Swallow	1	1	0	0	0
Cedar Waxwing	56	19	7	23	7
Chestnut-sided Warbler	1	0	1	0	0
Chimney Swift	1	0	1	0	0
Common Nighthawk	1	1	0	0	0
Common Yellowthroat	55	16	2	34	3
Connecticut Warbler	2	1	0	1	0
Eastern Bluebird	1	0	0	1	0
Golden-crowned Kinglet	2	0	1	1	0
Grasshopper Sparrow	1	0	0	1	0
Gray Catbird	11	3	1	6	1
Gray-cheeked Thrush	1	1	0	0	0
Great Crested Flycatcher	1	1	0	0	0
Hermit Thrush	4	0	0	4	0
Hooded Warbler	2	0	0	2	0
House Finch	1	0	0	1	0
Indigo Bunting	53	13	3	34	3

Kentucky Warbler	4	0	0	4	0
Louisiana Waterthrush	2	0	0	2	0
MacGillvray's Warbler	1	1	0	0	0
Magnolia Warbler	7	1	0	6	0
Mourning Dove	6	3	0	2	1
Northern Cardinal	121	3	7	92	19
Northern Mockingbird	2	1	1	0	0
Northern Parula	3	1	0	2	0
Northern Waterthrush	5	0	1	4	0
Ovenbird	24	1	1	19	3
Painted Bunting	2	0	0	1	1
Palm Warbler	1	0	0	0	1
Prairie Warbler	1	0	0	1	0
Prothonotary Warbler	26	7	1	18	0
Red-bellied Woodpecker	1	1	0	0	0
Red-eyed Vireo	5	1	1	3	0
Red-winged Blackbird	1	0	0	1	0
Rose-breasted Grosbeak	3	1	0	2	0
Ruby-throated Hummingbird	1	0	0	0	1
Scarlet Tanager	3	2	0	1	0
Spot-breasted Oriole	2	1	0	1	0
Summer Tanager	1	0	1	0	0
Swainson's Thrush	8	2	0	4	2
Swainson's Warbler	4	0	0	4	0
Swamp Sparrow	2	1	0	1	0
Tree Swallow	1	0	0	1	0
Tufted Titmouse	1	0	0	1	0
Veery	4	0	0	3	1
White-eyed Vireo	1	0	0	1	0
White-throated Sparrow	1	1	0	0	0
Wood Thrush	3	0	1	2	0
Yellow Warbler	2	1	0	1	0
Yellow-bellied Sapsucker	2	0	0	2	0
Yellow-billed Cuckoo	1	0	0	0	1
Yellow-rumped Warbler	7	0	0	7	0
Yellow-throated Vireo	2	0	0	2	0