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EFFECTS OF AGE AND WEAR ON WING LENGTH OF WOOD-WARBLERS

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Abstract.—We examined changes in the wing length of individual wood-warblers of four species caught at Powdermill, Pennsylvania. Wing length declined significantly from spring arrival to the beginning of the prebasic primary molt, presumably due to wear. Wing length also declined over the previous winter, but at a slower rate than during the summer. Feathers abraded more rapidly in females than males and in juveniles than adults. In all four species, wing length increased from the second to the third summer, corresponding to replacement of juvenal primaries. Wing length apparently continued to increase in subsequent molts in the Yellow-breasted Chat (*Icteria virens*), but not in the other three species. Overall, most changes were small relative to measurement error; a more precise measuring technique would facilitate detecting differences between ages, sexes, and species.

EFECTO DE LA EDAD Y EL DESGASTE EN EL LARGO DEL ALA DE EMBERÍSIDOS (EMBERIZIDAE)

Resumen.—Se examinaron los cambios en la longitud del ala de cuatro especies de Passeriformes capturados en Powdermill, Pennsilvania. El largo del ala disminuyó significativamente desde la llegada primaveral hasta el comienzo de la muda prebásica primaria, probablemente debido a desgaste. Durante el invierno se notó también una disminución en el largo del ala, pero en menor grado que durante el verano. Las plumas exhibieron mayor desgaste en hembras que en machos y en juveniles que adultos. En todas las especies estudiadas el largo del ala aumentó entre el segundo y tercer verano de su vida, correspondiendo esto al remplazo de las primarias juveniles. En *Icteria virens* el largo del ala aparentemente siguió incrementandose en mudas subsiguientes, aunque esto no fue notado en las otras especies estudiadas. Del trabajo se desprende que la mayoría de los cambios son pequeños y podrían estar relacionados con errores de medidas. Técnicas más precisas prodrian facilitar el que se puedan detectar diferencias en tamaños entre especies, y aves de diferente edad o sexo.

Wing length is probably the most frequently taken measurement on birds, especially by bird banders. It is often used as an indicator of overall size or for distinguishing races or sexes within a species. However, unlike skeletal elements, which are thought to be fully grown within a few months of fledging (but see McGillivray and Johnston 1987), feathers are replaced periodically and could change in length with each molt. Furthermore, feathers are subject to abrasion and breakage which may alter their length. In order to use wing length as a reliable indicator of size, the extent and phenology of change in this measurement during the life of the bird must be understood.

Changes in wing length can be examined indirectly by analyzing mean wing lengths for different age classes in a population. Many such studies have found that adults have longer wings than juveniles (e.g., Alatalo et al. 1984; Buckholtz et al. 1984; Mueller et al. 1981a, b; Nisbet et al. 1963), although in some hummingbirds the reverse is true (Ewald and Rohwer 1980). Similarly, measurements of birds taken from the same location at different times of the year have shown significant shortening of the wing between molts (Mueller et al. 1981a). However, such comparisons between means of different samples have limitations in interpretation. Changes in individuals are confounded with changes in the composition of the population, due to differential immigration or mortality related to size (Fleischer and Johnston 1982, McGillivray and Johnston 1987) or changing sex ratios (Thorne 1975). Furthermore, changes with age cannot be detected beyond the oldest class that can be identified based on plumage.

A few studies have examined changes in the wing lengths of individually marked wild birds. In general, comparisons between succeeding generations of feathers have confirmed that wing length increases after the first primary molt (Pienkowski and Minton 1973, Smith et al. 1986, Stewart 1963). Furthermore, studies on two species have shown that wing length continues to increase in subsequent molts: Red Knots (*Calidris canutus*; Pienkowski and Minton 1973) and Reed Warblers (*Acrocephalus scirpaceus*; Thorne 1975). Analyses of change within a single plumage have shown a significant decrease in wing length between molts for several species, in some cases up to 4% (Flegg and Cox 1977, Norman 1983, Pienkowski and Minton 1973, Thorne 1975).

However, wing length changes have been documented for a very limited number of species, and few comparisons of patterns of change between related species have been made. In this paper we examine and compare changes in wing length of individuals of four species of paruline warblers captured repeatedly in western Pennsylvania.

METHODS

Wing length was measured on birds captured at the banding station operated by the Carnegie Museum of Natural History at its Powdermill Nature Reserve in the foothills of the Allegheny Mountains in western Pennsylvania. A detailed description of the banding operation is given by Clench (1981) and Leberman and Wood (1983). The data analyzed here were collected between 1961 and 1985, mostly by one individual (R. C. Leberman). Wing length was measured as the distance from the bend of the wing to the tip of the longest primary without straightening the camber of the feather—i.e., the unflattened wing chord. Measurements were taken to the nearest 0.5 mm using a metal ruler with a fixed stop at one end. Birds in which the longest primary was broken, bent, severely abraded, or incompletely grown, were not measured.

Sex of each bird was determined based mainly on plumage characteristics. In the autumn, birds were aged as hatching year (HY) or after hatching year (AHY) by the degree of skull pneumatization. In spring and early summer, many second year (SY) birds could be distinguished from after second year birds (ASY) by the presence or absence of juvenal feathers, especially primary coverts. The remainder were classified as AHY. The age of recaptures was calculated from the age at original banding.

We restricted analysis to the four warbler species with more than 20 birds measured one year apart: Golden-winged Warbler (*Vermivora chrysoptera*), Yellow Warbler (*Dendroica petechia*), Common Yellowthroat (*Geothlypis trichas*), and Yellow-breasted Chat (*Icteria virens*); all nested near the banding station. Adults of all four species molted their primaries in late summer. Most juvenile chats and some juvenile yellowthroats molted at least their outer primaries. Chats, yellowthroats, and Golden-winged Warblers did not complete their molt until August or September, so wing lengths taken prior to the end of July were assumed to be based on old primaries. Yellow Warblers molted earlier, and some may have completed their molt by the end of July, so July measurements were excluded for this species. Lengths of fully grown wings measured after the end of August were assumed to represent new primaries for all four species.

We analyzed changes in wing length both within a molt cycle and from one molt to the next. We also assessed variation due to measurement error. For the analysis of change within the molt cycle (shortening of wing length due to wear or breakage) we used the earliest and latest measurement for each bird within a given cycle. We estimated the average rate of change for each species by linear regression of the change in wing length against the interval between captures, with the intercept fixed at the origin. We used analysis of covariance to test for differences in rates of change among species, sexes, ages, and seasons. Estimates of change in this analysis are minima because birds with extreme feather wear were not measured (to reduce biases in using wing length for other purposes). We could not determine the extent of such extreme feather wear, because the reason for not measuring a bird was frequently not recorded; at least 5% of birds that were measured once, were not measured at the final capture within a molt cycle because of worn primaries. The change in wing length of an individual from one plumage to the next was estimated by comparing the length in one year with the length in the same season the following year. The average wing measurement was used for any bird that was measured several times within the same season. Some individual birds that were captured over more than two years provided data points for more than one age class in these analyses.

RESULTS

Consistency of measurements.—Of 313 pairs of measurements taken on the same bird within 5 d, 30% did not differ, 33% differed by 0.5 mm, and 25% differed by 1 mm. The remaining 12% differed by 1.5–4 mm. There was no significant difference in the number that decreased (116)

TABLE 1. Decline in wing length of warblers over the period between April and July (S), and over the winter (W). All ages and sexes were combined for the analysis (sample size in parentheses).

Species	Season	Rate ± SE (mm/30 d)	P^a
Golden-winged Warbler	S	−0.35 ± 0.11 (87)	0.001
Yellow Warbler	S	−0.15 ± 0.14 (106)	0.15
Yellow-breasted Chat	S	−0.37 ± 0.13 (85)	0.003
Common Yellowthroat	S	−0.19 ± 0.05 (321)	<0.0003
	W	−0.05 ± 0.01 (133)	<0.0001

[a] Probability that decline could be zero (1-tailed test).

and increased (102; sign rank test $P = 0.29$). Measurable changes in wing length are unlikely to occur in such a short period, with the occasional exception of breakage of the tip of the longest primary. The most likely sources of the larger changes were bent or wet wings which shorten or lengthen the wing, respectively, and recording errors. There is no reason to believe these errors would cause any bias with respect to age or season, but they do increase the standard errors of estimates of average changes, thus reducing the power of comparisons between groups.

Changes between molts.—Wing length decreased throughout the summer in all four species, although the regressions were only significant in three species (Table 1). Wings of Yellow-breasted Chats and Golden-winged Warblers appeared to wear more rapidly than the other two species, but the differences among species were not statistically significant ($F_{3,595} = 1.0$, $P = 0.4$).

In all four species, feather wear was slightly greater in females than males (Table 2). In a combined analysis, the differences were not quite significant if the species were treated as blocks ($F_{1,594} = 3.46$, $P = 0.06$), though they were barely significant if the species term (which was not significant—see above) was omitted ($F_{1,597} = 4.13$, $P = 0.04$). The sexual differences were most marked for the Golden-winged Warbler (Table 2), but none of the individual differences is significant at the critical value

TABLE 2. Sexual differences in the decline in wing length between April and July (sample size in parentheses).

Species	Rate ± SE (mm/30 d) Females	Rate ± SE (mm/30 d) Males	P^a
Golden-winged Warbler	−0.81 ± 0.25 (19)	−0.19 ± 0.12 (68)	0.015
Yellow Warbler	−0.17 ± 0.34 (45)	−0.15 ± 0.15 (61)	0.95
Common Yellowthroat	−0.27 ± 0.08 (92)	−0.15 ± 0.07 (229)	0.30
Yellow-breasted Chat	−0.42 ± 0.17 (37)	−0.31 ± 0.20 (48)	0.68

[a] Probability that sexes could have the same rate of wear of wing length (2-tailed test).

TABLE 3. Changes in wing length between molts in different age classes of Common Yellowthroats (sample size in parentheses).

Season	Age	Rate ± SE (mm/30 d)	P^a
Summer[b]	ASY	−0.24 ± 0.079 (121)	0.0015
	SY	−0.32 ± 0.094 (53)	0.0006
Winter[b]	AHY	−0.026 ± 0.018 (64)	0.07
	HY	−0.058 ± 0.014 (63)	0.0001

[a] Probability that decline could be zero (1-tailed test).
[b] Differences between ages within each season in the decline in wing length were not significant (2-tailed tests: summer, $F = 0.35$, $P = 0.55$; winter, $F = 1.96$, $P = 0.16$).

appropriate for four simultaneous comparisons using the Bonferroni procedure ($P = 0.0127$).

The rate of overwinter wear could be estimated only for the Common Yellowthroat, which was the only species with more than a few individuals measured after the autumn molt and again the following spring. In this species, wing length declined significantly over the winter (Table 1), but at a significantly slower rate than during the summer ($F_{1,432} = 6.0$, $P < 0.02$).

The yellowthroat was also the only species with data adequate to examine the relationship between age and feather wear. Feather wear appeared to be greater for immature birds than adults over both the summer and winter, but the differences were not statistically significant (Table 3). The effect of wear on juvenal primaries during the winter may be underestimated, however, if any of the birds in our sample had molted their longest primaries after being measured in autumn. Such individuals may actually have longer primaries in spring, because replacement feathers are often longer than juvenal feathers (see below).

Changes with age and between plumages.—The pattern of change in wing length between years depended significantly on the initial age of the bird for the Golden-winged Warbler, Yellow Warbler, and Common Yellowthroat (Table 4). Wing length increased significantly in SY and AHY birds but not in ASY birds. The average increase was generally greater in the SY category than for the AHY birds. This is expected because the latter is almost certainly a composite of SY and older (ASY) individuals. In Yellow-breasted Chats, wing length increased significantly in AHY birds (no SY individuals were distinguished) and almost significantly in ASY birds ($P = 0.06$). Because most or all chats replace their outer primaries in their first autumn (Pyle et al. 1987), these data indicate that wing length of chats continues to increase for at least one molt after the first prebasic molt.

Some of the differences between SY and ASY wing lengths measured in spring could be due to greater wear on juvenal primaries over the winter. However, if we use the estimates for overwinter wear in the

TABLE 4. Mean (±SE) changes in wing length (mm) of birds recaptured during the same season after one year (sample sizes in parentheses).

Season/ Species	Age at first capture		
	SY	AHY	ASY
Spring/Summer			
Golden-winged Warbler	2.18 ± 0.16 (3)	0.67 ± 0.38 (17)*	−0.04 ± 0.15 (25)
Yellow Warbler	1.54 ± 0.47 (7)*	1.11 ± 0.28 (15)**	0.02 ± 0.11 (30)
Yellow-breasted Chat	—	0.91 ± 0.37 (12)*	0.43 ± 0.21 (14)†
Common Yellowthroat	1.08 ± 0.20 (17)***	1.02 ± 0.20 (37)***	−0.04 ± 0.13 (59)
Autumn			
Common Yellowthroat	1.51 ± 0.18 (26)***		0.22 ± 0.25 (15)

† $P < 0.10$ that change could be zero (2-tailed sign-rank test).
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.0001$.

Common Yellowthroat (Table 3), multiplied over 10 months, juvenile wings would decrease about 0.32 mm more, on average, than adult wings, which represents only 30% of the observed difference of 1.06 mm. Furthermore, data for Common Yellowthroats measured in the autumn (before any substantial wear could have taken place) and recaptured the following autumn also show that wing length increased significantly in young birds but not in older birds (Table 4).

DISCUSSION

Changes between molts.—The significant decrease in wing length between molts is probably due to abrasion. Burtt (1986) suggested that much feather wear may occur from airborne particles colliding with feathers during flight. Brushing against branches and other solid objects would add to this wear. The data for the Common Yellowthroat show a greater rate of wear in the summer, when the feathers are older, than over the winter. One explanation for this is that the rate of shortening of a feather may be related to how worn the tip is; worn feathers may shorten much faster than fresh feathers. Worn feathers may be especially susceptible to breakage of the tips from contact with solid objects such as branches or foliage. In addition, old feathers may lose some of their resiliency and become more brittle after prolonged exposure to the sun (Bergman 1982). Finally, the greater rate of wear in the summer may be due in part to higher densities of airborne particles (e.g., pollen grains) on the breeding grounds, or greater activity of the birds during nesting.

We are not aware of any previous reports of sexual differences in feather wear. The indications of greater feather wear in these female warblers, while not conclusive, suggest a need for further research. Differences in the strength of feathers or differences in activity levels of the sexes during breeding could both affect wear. Greater wear on juvenal feathers than those of adults, as seemed to occur in yellowthroats, has previously been reported for Sanderlings (*Calidris alba*; Pienkowski and Minton 1973). Again, such differences in wear could reflect either weaker juvenal primaries or differences in behavior (e.g., less skill at avoiding obstacles). The relative strength of the feathers could easily be tested in the laboratory but further data are required on the behavior of young birds to test the alternative hypothesis.

There were some indications that species differ in their rates of feather wear. Several morphological and behavioral factors could influence wear, including feather color (Burtt 1986), wing shape, and activity patterns. Habitat differences in either breeding or non-breeding seasons could also contribute to differing rates. Further data are required both to confirm the interspecific differences, and to determine which factors are most important in affecting wear.

Changes between succeeding plumages.—The observed increases in wing length after the first prebasic primary molt agree with previous studies on other species of birds (Alatalo et al. 1984, Pienkowski and Minton 1973, Stewart 1963). However, the Yellow-breasted Chat was the only species that showed any sign of further increase in subsequent molts.

Two hypotheses have been proposed to explain the shorter wing lengths of juveniles (Alatalo et al. 1984). The first is that nestlings are under greater nutrient limitation or stress, perhaps because they have to grow all their feathers simultaneously, so they cannot grow long primaries. There is evidence from both laboratory and field experiments that nutrient limitation and parental care affect nestling growth, including wing length (Boag 1987, James 1983). Few studies have been done on primary molt in adults, but extreme malnutrition (Murphy et al. 1988) and protein availability (Pehrsson 1987) affect wing length in captive birds.

An alternative hypothesis is that juveniles have different aerodynamic requirements from adults, and the shorter wing length is, in fact, adaptive, and therefore genetically programmed. Alatalo et al. (1984) found that the outer primary of four European passerines was actually longer in juveniles than in adults, although the wing length (determined by the longest primary) was shorter. The outer primary of juvenile Hairy (*Picoides villosus*) and Downy (*P. pubescens*) woodpeckers is also much longer and of different shape than that of adults (George 1972). In the Eurasian Sparrowhawk (*Accipiter nisus*), the juvenal secondaries are longer than those of adults, with the result that total wing area is greater in juveniles, despite a shorter wing (Newton 1986). In this species, as well as Cooper's (*A. cooperii*) and Sharp-shinned Hawks (*A. striatus*), the juvenile tail is also longer than that of adults (Mueller et al. 1981a, b; Newton 1986). These observations are inconsistent with the nutrient limitation hypothesis, which would predict that feathers in all the tracts should be shorter. Alatalo et al. (1984) suggested that greater wing slotting in juvenile passerines, created by a longer outer primary, increases lift and maneuverability. Similarly, the shorter, broader wings and longer tail of juvenile accipiters provide greater lift, allowing slower, more efficient flight (Newton 1986). Only after the birds have become experienced fliers do they acquire the longer, narrower wings of adults.

Continued increases in wing length after the first year, as seem to occur in the Yellow-breasted Chat and a few other species (Pienkowski and Minton 1973, Thorne 1975) may have similar explanations. Older birds may increase in dominance status or know better foraging areas, thus acquiring more nutrients for feather formation during molt (Pehrsson 1987). Alternately, the increase may be genetically programmed, although changes in aerodynamic requirements after the first year seem unlikely. Further data are required to clarify the patterns of change in individuals older than two years and to determine whether these changes in length are correlated with changes in wing shape.

CONCLUSIONS

Primary wear and age both have significant effects on the wing length of individual birds, and need to be considered if wing length is to be used as an index of size. There were indications from this study that the magnitude of these effects varies with season, sex, and species. However, correcting for these effects is difficult, owing to the high standard error of the estimates. Further data are required to refine these estimates, and to obtain similar information for other species. A more precise measure of wing length, such as measuring the length of the longest primary from its point of insertion (Berthold and Friedrich 1979, Jenni and Winkler 1989), would facilitate such studies, and should be considered for future research on feather wear or growth.

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