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AGE, SEX, AND SEASONAL DIFFERENCES IN SIZE OF COOPER'S HAWKS

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In North America, the Goshawk (*A. gentilis*) is the largest and least sexually dimorphic member of the genus *Accipiter,* and the Sharp-shinned Hawk (*A. striatus*) is the smallest and most sexually dimorphic. In both species, adults have longer wings, shorter tails, and weigh more than juveniles (Mueller et al. 1976, 1979). In this paper we show that the Cooper's Hawk (*A. cooperii*), which is intermediate in both size and extent of sexual dimorphism, shows comparable differences in measurements between adults and juveniles. Our primary purpose in this paper is to examine seasonal variations in weight and other measurements of Cooper's Hawks, particularly whether or not juveniles achieve adult weight in spring, before they assume the adult plumage. The Cooper's Hawk is the only species of *Accipiter* for which we have an adequate sample of measurements for both spring and fall. We also present criteria for determining the age and sex of Cooper's Hawks, compare age and sex dimorphism in the three species of *Accipiter,* and discuss the probable adaptive significance of age differences in size.

METHODS

Source of data.—We trapped 201 Cooper's Hawks during spring migration and 219 during fall migration at the Cedar Grove Ornithological Station in the years 1953–1975. The station is on the western shore of Lake Michigan about 70 km north of Milwaukee, Wisconsin. Due to occasional errors, not all measurements were recorded for all birds, and the sample sizes vary slightly.

A description of the Cedar Grove region can be found in Mueller and Berger (1966). Trapping methods are described by Bub (1974) and measuring techniques are described by Mueller et al. (1976). For a general account of hawk migrations in fall at Cedar Grove see Mueller and Berger (1961); for spring migrations see Mueller and Berger (1969).

Age criteria.—A bird entirely in the brown (juvenal) plumage is a juvenile or HY-SY (Hatching Year until 31 December, Second Year after 1 January). The entire dorsal surface, including the head, back, wings, and tail is brown and the underside is whitish with brown streaks. The molt from the juvenal plumage into the first adult (basic) plumage is not completed until late summer or fall of the second year.

Adults are blue-gray above, except for a brownish cast on the back of females, and the undersides are white, barred with a reddish brown. A gray-plumaged bird with any brown feathers is more than one, but less than two years old, and is an Adult I or SY-TY. An entirely gray-plumaged bird with two generations of gray feathers (feathers produced by two different molts in two different years) is an Adult II or ASY-ATY.

An entirely gray-plumaged bird with only one generation of feathers is an adult of unknown age or AHY. A few of these birds can be aged by eye color (see below).

Extremely careful examination of the bird, in good light, is necessary to differentiate ASY from AHY. In autumn we were able to determine the age of 47% of the adult males and 70% of the adult females. Only 7% of the adults could be aged in spring. It is necessary to examine each flight feather (remex and rectrix) closely for differences in wear and coloration. Feathers of a previous generation usually show noticeably more wear, particularly in the rectrices, and a subtle fading in color can usually also be seen. Cooper's Hawks take several months to complete a molt, and feathers molted early (innermost primaries) may show more wear than feathers molted later (outermost primaries). Rectrix molt appears to be somewhat erratic; the central (No. 1) and outer (No. 6) are almost invariably replaced by early fall, while numbers 2 and 5 appear to be the last to be molted. The presence of a few feathers of a new generation, particularly in the body plumage, are usually not the result of a molt because feathers pulled out in an accident are replaced without delay by feathers of the next plumage.

In the 3 North American species of *Accipiter,* eye color changes with age, progressing from gray to pale yellow, orange, and red. This color change is poorly understood and shows considerable individual variation. Ten Adult I males all had light orange irides (approximately equivalent to color 18, orange-yellow of Smithe 1975) and 6 Adult II males all had orange irides (ca. color 17, spectrum orange of Smithe). Two Adult I females had yellow irides and 9 had light orange eyes; 1 Adult II female had light orange eyes; 1 had orange, and 2 had dark orange (color 16, chrome-orange of Smithe). This small sample suggests that males with light orange irides can be aged as Adult I, and those with orange or darker irides can be aged as Adult II. It also appears that adult females with yellow irides can be aged as Adult I and those with irides of orange or darker can be aged as Adult II. Females with light orange irides cannot be aged. We urge caution in using eye color for determining age. In our entire sample of eye colors of fall Cooper's Hawks, including birds that could not be aged by molt, we found irides of the various shades of red in only 2% of the adults. This is in sharp contrast to the 14% found in Goshawks and the 17% in Sharp-shinned Hawks.

Sex criteria.—Sex of birds was determined by an examination of the distributions of measurements as explained in detail by Mueller et al. (1976). The measurements are presented in Tables 1 and 2, and sex criteria, with confidence limits, in Table 3. Data from Adult I, Adult II, and adults of unknown age were grouped in these tables because we found no significant difference in any measurement between Adult I and Adult II. Either wing chord or weight can be used to determine, with near certainty, the sex of both adult and juvenile Cooper's Hawks whether caught in spring or fall.

TABLE 1. Autumn measurements of Cooper's Hawks.[1]

Measurement	Age	Males n	Males Mean ± SD (range)	Females n	Females Mean ± SD (range)
Tail length (mm)	Juv.	53	196 ± 5.2 (185–207)	58	221 ± 7.1 (210–238)
	Adult	51	191 ± 5.4 (180–202)	58	217 ± 5.4 (207–239)
Wing chord (mm)	Juv.	52	234 ± 4.5 (224–247)	59	266 ± 5.2 (254–275)
	Adult	48	238 ± 5.4 (225–246)	56	270 ± 6.6 (258–292)
Weight (g)	Juv.	53	335 ± 26.5 (292–389)	58	499 ± 39.8 (413–598)
	Adult	51	349 ± 19.6 (297–380)	57	529 ± 36.1 (460–588)

[1] Within an age class, males differ significantly from females in every measurement (t-test, $P < 0.0001$). Within each sex, adults differ significantly from juveniles in every measurement (t-test, $P < 0.05$).

RESULTS

Changes in size with age.—In both autumn and spring, adult Cooper's have longer wings, shorter tails, and weigh more than juveniles, and all differences are statistically significant (Tables 1 and 2). However, the use of the seasonal means given in Tables 1 and 2 might be questioned because: (1) juveniles of both sexes show significant fits to linear regressions of weight on calendar date, increasing in fall and decreasing in spring; (2) juvenile females show significant fits to linear regressions of wing chord on calendar date, decreasing in both seasons; (3) adults of both sexes fail to show a significant fit to linear regressions of either weight or wing chord on calendar date in either spring or fall; (4) adults migrate later in fall and earlier in spring than do juveniles (Table 4). In Sharp-shinned Hawks we found significant fits to linear regressions of weight and wing chord on calendar date in all ages and sexes (Mueller et al. 1979), and in Goshawks we found a significant fit to a linear regression of weight on calendar date in juveniles and Adult II, but not in Adult I.

The obvious change in weight with calendar date and the age differences in timing of migration lead to the question of whether the mean seasonal differences are an artifact of comparing samples which differ primarily in having been taken at different times in the season. The lack of a significant fit to linear regressions in the adults led us to partition the season into 3 parts, with the mid-season portion representing an attempt to maximize the number of both adults and juveniles occurring within a reasonable calendar interval (Tables 5–8).

TABLE 2. Spring measurements of Cooper's Hawks.[1]

Measurement	Age	Males n	Males Mean ± SD (range)	Females n	Females Mean ± SD (range)
Tail length (mm)	Juv.	33	191 ± 6.3 (173–199)	78	217 ± 6.0 (203–232)
	Adult	31	188 ± 4.4 (175–195)	50	212 ± 6.3 (200–226)
Wing chord (mm)	Juv.	32	231 ± 4.3 (221–240)	75	263 ± 5.6 (251–273)
	Adult	33	236 ± 5.5 (226–244)	51	266 ± 6.8 (253–281)
Weight (g)	Juv.	33	331 ± 20.5 (286–389)	78	535 ± 42.0 (454–652)
	Adult	32	347 ± 23.6 (311–411)	52	553 ± 44.2 (468–643)

[1] Within an age class, males differ significantly from females in every measurement (*t*-test, $P < 0.0001$). Within each sex, adults differ significantly from juveniles in every measurement (*t*-test, $P < 0.05$).

Comparisons of mean weights within partitioned calendar intervals show no significant difference between juvenile and adult males in autumn (Table 5). This is curious because adult males have significantly longer wing chords than juveniles during the mid-fall interval (Table 6), the very interval in which they fail to show a difference in weight. Juvenile males show a significant increase in weight between early and mid-fall (Table 5); we were unable to find any significant change in

TABLE 3. Sexing criteria and confidence intervals for Cooper's Hawks.

Measurement	Season	Age	Confidence interval %	Upper limit for males	Lower limit for females
Tail length (mm)	Fall	Juv.	95.86	205	206
		Ad.	98.54	203	204
	Spring	Juv.	99.60	203	204
		Ad.	97.74	197	198
Wing chord (mm)	Fall	Juv.	99.86	248	249
		Ad.	99.24	251	252
	Spring	Juv.	99.84	244	245
		Ad.	98.54	248	249
Weight (g)	Fall	Juv.	98.92	395	396
		Ad.	99.94	419	420
	Spring	Juv.	99.88	397	398
		Ad.	99.72	415	416

TABLE 4. Median dates of occurrence of Cooper's Hawks at Cedar Grove Ornithological Station.

Age	Sex	Fall	Spring
Juvenile	Male	1 Oct.	2 May
Adult	Male	12 Oct.	12 Apr.
Juvenile	Female	25 Sep.	21 Apr.
Adult	Female	12 Oct.	14 Apr.

adult males during the autumn no matter how we partitioned the data. The increase in weight of juvenile males could be the result of either an increase in muscle and other organ weight or fat deposition. A comparison of mean weights for the entire season between fall and spring shows no significant difference for either adult or juvenile males (Table 9), suggesting that the weight change in juveniles in autumn is permanent and not due to fat deposition. However, the weights of juvenile males show a considerable decline between mid- and late spring (Table 7), and although this difference is not statistically significant, a comparison of the weights of the first 16 juvenile males taken in spring with the weights of the last 17 does show a significant difference (340 ± 18.5 g vs. 323 ± 19.4 g, $t = 2.47$, $P < 0.05$). The weight of late spring juvenile males (Table 7) is slightly less than that of early autumn (Table 5), and it appears that the increase in weight in fall and the decrease in spring is probably due to fat deposition and loss. Adult males show no significant increase in fall and no decrease in spring, no matter how we partition the data, suggesting that there is very little fat deposition and loss. We thus conclude that adult males have a greater lean body weight than juveniles in autumn but that fat deposition in the juveniles obscures this difference.

In spring, comparisons of weights of juvenile and adult males in the

TABLE 5. Cooper's Hawk fall weights (g) partitioned by calendar date.

Sex	Calendar interval	Adults n	Adults Mean ± SD	Juveniles n	Juveniles Mean ± SD
Males	8 Sep–26 Sep	1	355	23	322.6 ± 18.35
	27 Sep–25 Oct	45	347.4 ± 19.77	28	342.8 ± 22.82[1]
	26 Oct–22 Nov	5	358.4 ± 19.63	2	370.5 ± 26.16
Females	29 Aug–12 Sep	0		13	488.1 ± 35.56
	13 Sep–21 Oct	48	525.2 ± 35.59[2]	40	497.7 ± 40.28
	22 Oct–19 Nov	9	555.9 ± 25.47[1]	5	540.6 ± 19.54[1]

[1] Significantly greater than the mean weight for the preceding calendar interval, t-test, $P < 0.05$.

[2] Significantly greater than weight of juveniles, t-test, $P < 0.001$. All other differences insignificant $P > 0.05$.

TABLE 6. Cooper's Hawk fall measurements of wing chord partitioned by calendar date.

Sex	Calendar interval	Adults		Juveniles	
		n	Mean ± SD	n	Mean ± SD
Male	8 Sep–26 Sep	0		23	234.7 ± 5.82
	27 Sep–25 Oct	43	237.9 ± 5.58[1]	27	233.4 ± 3.14
	26 Oct–22 Nov	5	237.0 ± 3.08	2	236.0 ± 4.24
Female	29 Aug–12 Sep	1	274	13	267.9 ± 4.85
	13 Sep–21 Oct	46	270.0 ± 6.84[1]	41	265.1 ± 5.14
	22 Oct–19 Nov	9	267.4 ± 5.83	5	263.0 ± 5.79

[1] Significantly greater than the mean for juveniles, *t*-test, $P < 0.001$. All other differences insignificant $P > 0.05$.

samples partitioned by calendar interval show no significant difference (Table 7). However, there are several peculiarities about the mid-spring sample on which the comparisons are based: (1) there is no significant difference in wing chord between adult and juvenile males during this calendar interval (Table 8), while there is a significant difference over the entire season (Table 2); (2) there is a significant decrease in wing chord of adult males between early and mid-spring while juvenile males show no change in wing chord with date (Table 8). The wing chord of adult males decreases 1.64% between early and mid-spring while the cube root of weight decreases only 0.56%. A 1.64% decrease in the cube root of weight would result in a weight of 331.8 g for mid-spring adult males, slightly less than the weight of juvenile males for the same calendar interval. Linear measurements do vary as a function of the cube root of weight and the above calculations suggest that adult males do not decrease appreciably in weight relative to size as the spring progresses, and therefore the lack of a difference in weight between adult and juvenile males in mid-spring is the result of a comparison of small adults with juveniles of normal size. The reduction in wing chord of adult males during the spring cannot be adequately accounted for by wear; adult males caught in spring have wing chords that are only a mean of 1.7 mm shorter than those taken in autumn (Table 9) while the difference between early and mid-spring is 3.9 mm (there are 182 days between the median dates of capture of adult males in fall and spring and only 17 days between the median dates of capture of adult males between early and mid-spring). We thus conclude that adult males have a greater lean body weight than juvenile males in spring.

Adult females weigh significantly more than juveniles in the mid-autumn partitioned sample (Table 5), and adult females also have a longer wing chord than juveniles in mid-autumn (Table 6). Adult females clearly weigh more than juveniles in autumn. Both adults and juveniles show a significant increase in weight between mid- and late fall, probably indicating fat deposition (Table 5).

TABLE 7. Cooper's Hawk spring weights (g) partitioned by calendar date.

Sex	Calendar interval	Adults		Juveniles	
		n	Mean ± SD	n	Mean ± SD
Male	2 Apr–12 Apr	20	348.7 ± 25.83	0	
	13 Apr–5 May	12	342.9 ± 19.87	27	334.4 ± 19.35
	6 May–18 May	0		6	317.3 ± 21.05
Female	17 Mar–2 Apr	5	580.4 ± 39.19	9	585.7 ± 42.59
	3 Apr–24 Apr	40	549.8 ± 43.78	36	545.8 ± 37.13[1]
	25 Apr–17 May	7	554.3 ± 49.37[2]	33	509.9 ± 28.56[1]

[1] Significantly lower than the mean weight of the preceding calendar interval, *t*-test, $P < 0.01$.
[2] Significantly greater than weight of juveniles, *t*-test, $P < 0.01$. All other differences insignificant $P > 0.05$.

In spring, adult females weigh more than juveniles only in the late spring partitioned sample (Table 7). However, this is also the only partitioned sample which shows a significant difference in wing chord (Table 8). A difference in wing chord is expected because it was found in the means for the entire season for spring (Table 2) and fall (Table 1), and in the mid-season partitioned sample for fall (Table 6). Juvenile females show a significant decrease in weight through the spring (Table 7); adult females do not, no matter how we partition the data. The loss in weight in juvenile females in spring is undoubtedly the result of loss of fat. We thus conclude that adult females exhibit a greater lean body weight than juveniles in spring. Both adult and juvenile females show significant decreases in wing chord during the spring (Table 8) and these decreases are in excess of what might be attributed to wear (cf.

TABLE 8. Cooper's Hawk spring measurements of wing chord partitioned by calendar date.

Sex	Calendar interval	Adults		Juveniles	
		n	Mean ± SD	n	Mean ± SD
Male	2 Apr–12 Apr	21	237.5 ± 5.39	0	
	13 Apr–5 May	12	233.6 ± 4.80[1]	26	231.4 ± 4.01
	6 May–18 May	0		6	230.3 ± 5.50
Female	17 Mar–2 Apr	4	272.5 ± 6.03	9	265.3 ± 5.70
	3 Apr–24 Apr	37	265.2 ± 6.17[2]	35	263.5 ± 4.99
	25 Apr–17 May	10	265.1 ± 7.94[3]	31	260.6 ± 5.75[2]

[1] Almost significantly less than the mean for the preceding calendar interval, *t*-test, $P > 0.05 < 0.06$.
[2] Significantly less than the mean for the preceding calendar interval, *t*-test, $P < 0.05$.
[3] Significantly greater than the mean for juveniles, *t*-test, $P < 0.05$.

TABLE 9. Difference between spring and fall measurements of Cooper's Hawks.[1]

Measurement	Age	Sex	Difference (g or mm)	%
Weight (g)	Juvenile	Male	−3.8	−1.13
	Juvenile	Female	+36.0[2]	+6.72
	Adult	Male	−2.1	−0.60
	Adult	Female	+23.0[2]	+4.21
Wing chord (mm)	Juvenile	Male	−4.2[2]	−1.23
	Juvenile	Female	−3.0[2]	−1.13
	Adult	Male	−1.7	−0.71
	Adult	Female	−3.9[2]	−1.44
Tail (mm)	Juvenile	Male	−4.8[2]	−2.46
	Juvenile	Female	−4.0[2]	−1.79
	Adult	Male	−3.0[2]	−1.55
	Adult	Female	−5.0[2]	−2.32

[1] Spring mean minus fall mean.
[2] Spring measurement differs significantly from fall measurement, *t*-test, $P < 0.05$.

Tables 8 and 9). It appears that larger females of both age groups have a tendency to migrate earlier in spring than smaller females.

All age and sex classes have shorter tails and wings in spring than in autumn (Table 9). These differences are statistically significant in all but the wing chord of males and undoubtedly represent wear on the feathers over the winter. Both adult and juvenile females weigh significantly more in spring than in autumn; males of both age groups are slightly, but not significantly, lower in weight in spring than in autumn (Table 9). However, if we compare samples partitioned by calendar date, only adult females show an increase in weight between early fall and late spring. No other age or sex group differs significantly in weight between early fall and late spring.

Wing loading helps give an indication of flight speed, maneuverability, and other aerodynamic characteristics. Total wing area of both wings can be estimated by the formula: wing area = $(\text{wing chord}/0.62)^2/1.93$ (Greenewalt 1962). The estimates of wing loading show that females have higher wing loadings than males (Table 10). In autumn, adults have higher wing loadings than juveniles, but by spring this age difference has virtually disappeared (Table 10).

If we estimate wing loadings for the partitioned calendar intervals in Tables 5–8, we find that juvenile males have heavier wing loadings in the mid-fall interval (0.467 g/cm^2) than adult males (0.455). This difference is undoubtedly the result of weight gain due to fat deposition in juveniles and the lack of weight gain in adults. Since adult males fail to show any appreciable increase in weight as the autumn progresses, while juveniles show a significant increase, it is reasonable to compare the wing loadings for the first 50% of the adults captured in autumn with the first 50% of the juveniles, thus comparing a sizeable sample of ju-

TABLE 10. Estimated mean wing area and wing loading of Cooper's Hawks.

Age	Season	Males		Females	
		Wing area[1] (cm^2)	Wing loading (g/cm^2)	Wing area[1] (cm^2)	Wing loading ($g–cm^2$)
Juvenile	Fall	738.6	0.449	950.4	0.525
	Spring	720.4	0.460	929.0	0.576
Adult	Fall	762.3	0.457	980.1	0.541
	Spring	751.2	0.461	951.9	0.581

[1] Estimated by the formulae from Greenewalt (1962): Wing area = $(\text{wing chord}/0.62)^2/1.93$. Estimate based on data in Tables 1 and 2.

veniles with little fat with adults with little fat, during approximately, but not quite, the same calendar interval. The mean wing loading of the 27 juvenile males taken between 8 and 30 September is 0.436 g/cm^2 and that of the 27 adults taken between 16 September and 12 October is 0.459, a considerable difference.

Adult females have heavier wing loadings than juveniles in mid- and late fall as was the case for wing loadings estimated from means for the entire autumn. In late spring, adult females have heavier wing loadings (0.585) than juveniles (0.557). There is no appreciable difference in the wing loadings of adult and juvenile males in mid-spring. However, we are again faced with the problem that juvenile males show a significant change in weight as the season progresses while adults show no appreciable change. If we compare the wing loading of the last half of the adult males captured in spring with that of the last half of the juvenile males taken, then we are comparing groups of birds with little fat taken within a reasonably similar, although not identical, calendar interval. The mean wing loading of the 16 adult males taken between 12 April and 5 May is 0.466 g/cm^2 and that of the 17 juveniles captured between 1 and 18 May is 0.448. We thus conclude that adults of both sexes have heavier wing loadings than juveniles, but that in males this difference is obscured through most of the spring and fall by the lack of appreciable fat deposition in adults.

Comparisons with other species.—The Sharp-shinned Hawk exhibits the greatest sexual dimorphism in every measurement and the Goshawk the least, except for tail length, in which Cooper's Hawks are about 1% less dimorphic than Goshawks (Table 11). Although differences generally are slight, adults tend to be more dimorphic than juveniles. If we eliminate from consideration the ratios of wing area and cube root of weight, which are derived directly from wing chord and weight, adults show greater dimorphism than juveniles in 9 of the 12 cases; the exceptions are wing chord and weight of Sharp-shinned Hawks and wing loading of Goshawks. The difference in sexual dimorphism between adults and

TABLE 11. Ratio of female to male measurements of 3 *Accipiter* species.[1]

Measurement	Age	Sharp-shinned Hawk[2]	Cooper's Hawk	Goshawk[3]
Tail	Juvenile	1.179	1.128	1.138
	Adult	1.182	1.138	1.156
Wing chord	Juvenile	1.186	1.134	1.085
	Adult	1.182	1.134	1.093
Weight	Juvenile	1.700	1.490	1.244
	Cube root	1.193	1.142	1.075
	Adult	1.692	1.520	1.245
	Cube root	1.192	1.150	1.075
Wing area	Juvenile	1.406	1.287	1.176
	Adult	1.397	1.286	1.195
Wing load	Juvenile	1.209	1.169	1.058
	Adult	1.212	1.184	1.043

[1] Autumn means.
[2] Data from Mueller et al. 1979.
[3] Data from Mueller et al. 1976.

juveniles exceeds 2% only once: in weight of Cooper's Hawks. This is particularly striking because Cooper's Hawks show no age difference in sexual dimorphism of wing chord. Thus, adult Cooper's Hawks appear excessively sexually dimorphic, or juveniles insufficiently dimorphic, in weight. Three additional differences in sexual dimorphism between adults and juveniles exceed 1%: Goshawk tail length and wing loading, and Cooper's Hawk wing loading.

Generally, Goshawks exhibit the greatest age dimorphism in measurements and Sharp-shinned Hawks the least (Table 12). The exceptions are: (1) the sequence is reversed for the wing chord of males, where Sharp-shinned Hawks exhibit the greatest age dimorphism and Goshawks the least, but differences in ratios are only 0.1 to 0.4%; (2) the weight of males, where Sharp-shinned Hawks are 1.4% more dimorphic than Cooper's Hawks, and Goshawks are 8.4% more dimorphic than Sharp-shinned Hawks—thus, male Cooper's Hawks appear to show too little age dimorphism in weight; (3) wing loading of males, where Cooper's Hawks show the least difference of the three species, an anomaly which is the result of the reduced age dimorphism in weight of the species.

Females tend to show greater age dimorphism than males. This is because of a simple algebraic relationship between age dimorphism and sex dimorphism. The greater sex dimorphism found in adults (Table 11) can be stated as the following inequality: A♀/A♂ > J♀/J♂. If we multiply both sides of this inequality by A♂ and by 1/J♀ we obtain the inequality: A♀/J♀ > A♂/J♂. Thus, greater sexual dimorphism in adults is linked with greater age dimorphism in females, and greater

TABLE 12. Ratio of adult to juvenile measurements of 3 *Accipiter* species.[1]

Measurement	Sex	Sharp-shinned Hawk[2]	Cooper's Hawk	Goshawk[3]
Tail	Male	0.984	0.973	0.962
	Female	0.987	0.981	0.978
Wing chord	Male	1.016	1.015	1.012
	Female	1.013	1.016	1.020
Weight	Male	1.055	1.040	1.144
	Cube root	1.018	1.013	1.046
	Female	1.052	1.062	1.147
	Cube root	1.017	1.020	1.046
Wing area	Male	1.033	1.032	1.026
	Female	1.027	1.031	1.041
Wing load	Male	1.024	1.018	1.117
	Female	1.026	1.030	1.101

[1] Autumn means.
[2] Data from Mueller et al. 1979.
[3] Data from Mueller et al. 1976.

sex dimorphism in juveniles is linked with greater age dimorphism in males. The exceptions to greater age dimorphism in females (Table 12) are in the same items that showed greater sexual dimorphism in adults (Table 11). In comparisons of ratios, as done above, it is thus impossible to state whether birds are showing excessive sexual dimorphism within an age group or excessive age dimorphism within a sex.

DISCUSSION

We have suggested in previous papers that the age differences in measurements of accipiters have adaptive significance (Mueller et al. 1976, 1979). The greater weight and wing loading of adults both permits and obligates them to fly faster than juveniles. The greater weight and speed of adults results in rapid pursuit and a more forceful strike at prey than is possible for juveniles. We presented data for Sharp-shinned Hawks (Mueller et al. 1979) which showed that the greater weight of adults was not due to a higher incidence of fat than in juveniles, and suggested that adults had a more massive flight musculature than juveniles. The longer wings and presumably higher aspect ratios of adults are a more efficient aerodynamic design than those of juveniles. Adults thus are more rapid, powerful, and higher performance fliers than juveniles. We have also suggested that the superior flight capabilities of adults would give them a competitive advantage in agonistic encounters with juveniles. This high performance of adults presumably requires and permits a greater food intake than in juveniles. The lighter wing loading of juveniles probably enables them to fly a given distance with less energy expenditure than adults. The shorter wings and longer tails of juveniles enhance maneuverability, obviously advantageous until the young acquire full expertise in flight and pursuit of prey. The longer tail also contributes somewhat to lift; in flapping flight the lift gained by a larger tail is undoubtedly more economical than having to flap larger wings. Thus, juveniles are economical and maneuverable fliers. The reduced maneuverability in adults may be overcome by experience and greater muscle power in the adults as compared with juveniles.

One of the purposes of this paper was to determine when juveniles achieved adult weight and wing loading: before or after the molt into the adult (basic) plumage. Do juveniles achieve adult weight in spring, when their experience in flight, pursuit, and capture of prey should be sufficient to permit it, or is the weight gain deferred until the molt into the adult plumage when changes in the lengths of flight feathers are "appropriate" to changes in body weight? It appears that the latter is true; the data partitioned by calendar date show clearly that although juvenile female Cooper's Hawks increase in weight and wing loading between fall and spring, adult females show changes of the same magnitude and the differences between adults and juveniles in spring and fall are virtually identical. The picture for males is confused by the apparent lack of fat deposition in adults in fall and hence no gain in weight as the season progresses. This results in no significant difference between the weights of juveniles and adults in mid-fall and a higher estimated wing loading in juveniles than in adults. The lack of weight gain in autumn in adult males is clearly an abnormality; we found weight gains in autumn in adult and juvenile, male and female Goshawks and Sharp-shinned Hawks (Mueller et al. 1976, 1979). This peculiarity of adult male Cooper's Hawks results in the anomalies of adults showing excessive sexual dimorphism and males showing insufficient age dimorphism when compared with the Goshawk and Sharp-shinned Hawk.

There are several other peculiarities in our data. Juveniles show a significant decrease in weight in spring as the season progresses but adults do not. The lack of a decrease in adult males is not surprising because they failed to gain weight in fall, but we have no explanation why only adult females are heavier at the end of spring migration than they are at the beginning of fall migration, other than to suggest that this represents a reserve of fat for breeding.

It appears that, in spring, larger Cooper's Hawks (as determined by wing chord) migrate earlier than smaller individuals. We suggest that the larger birds breed farther south than smaller individuals. In the northern hemisphere, birds with contiguous subspecies or populations breeding in the north are smaller, migrate farther, and have shorter wing chords than those breeding in the south (Averill 1920, Salomonsen 1955). This generalization appears to hold for *Accipiter*: of the 50 or more species only one has subspecies which obviously breed farther north and migrate farther than contiguous southern subspecies. The

North American subspecies of the Sharp-shinned Hawk increase with size southward until a discontinuity in breeding range in the Isthmus of Tehuantepec (Brown and Amadon 1968). In addition, the North African race of the Sparrowhawk, *A. nisus punicus,* is larger than the nominate European subspecies and is separated from it only by the Straits of Gibraltar (Brown and Amadon 1968). At the longitude of Cedar Grove, the breeding range of the Cooper's Hawk extends only into northern Michigan and Western Ontario (450 to 1000 km N and NW) which does not provide a great deal of latitude for variation in size. However, the breeding range extends into central Alberta, 2500 km NW (A.O.U. 1957). We have little knowledge of the breeding localities of the Cooper's Hawks seen in migration at Cedar Grove, but an adult Sharp-shinned Hawk banded in fall migration at Cedar Grove was recovered during the following breeding season in central Alberta (Mueller and Berger 1967). We believe it is likely that both species of *Accipiter* avoid the Great Plains by migrating SE from western Canada.

Juvenile males do not show a change in size as the spring progresses. We suspect that this is because juvenile males rarely breed and possibly do not migrate as regularly in spring as adults and juvenile females. Juvenile males pass through Cedar Grove considerably later than any other age/sex class, and most juvenile males pass through southern Wisconsin after the time adults are on breeding territories. Cooper's Hawks only occasionally breed in the juvenal plumage, and apparently females do so more frequently than males. We have been unable to find an account of males breeding in the juvenal plumage, but Bent (1937) lists a female breeding and Meng (1951) found juvenile females in 2 of 34 breeding pairs. A greater incidence of females breeding in the juvenal plumage than males seems to be true of other *Accipiter*; McGowan (1975) found juvenile females at 36% of the Goshawk nests studied in Alaska in 1971; no juvenile males were seen at any nest in the 4 years of his study.

If populations of large and small Cooper's Hawk are temporally segregated in spring migration, as we have suggested, it is curious that they show no segregation during fall migration.

SUMMARY

The sex of Cooper's Hawks can be determined with near certainity by wing chord or weight. The age of adults can be determined in autumn by plumage in 47% of the males and 70% of the females; only 7% of the adults can be aged in spring. Juveniles have significantly shorter wings, longer tails, and weigh less than adults; these differences persist through spring migration. Thus, young birds apparently do not achieve adult weight until they molt into adult plumage. All age and sex groups except adult males gain weight during the fall, presumably due to fat deposition. Juveniles lose weight during spring, presumably due to fat loss; adults do not. The lack of weight change with season in adult males is anomalous; other species of *Accipiter* show a weight gain in

adult males in fall. Estimated wing loadings are higher in females and adults, with exceptions in adult males because of their failure to show a weight gain in autumn. We discuss the possible adaptive significance of age differences in measurements. Of the 3 species of *Accipiter* in North America, the Sharp-shinned Hawk exhibits the greatest sexual dimorphism and the Goshawk the least, except for tail-length, in which the Cooper's Hawk is the least dimorphic. Longer-winged, and presumably larger, Cooper's Hawks migrate earlier in spring than smaller individuals. We suggest that the smaller birds breed at more northern latitudes than the larger individuals.

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