

RELATIONSHIP OF BIB SIZE TO AGE AND SEX IN THE BLACK-CAPPED CHICKADEE

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Abstract.—The size and shape of the black bib in Black-capped Chickadees varies among individuals and may signal information about age and sex, as found in other species with similar plumage badges. By photographing and measuring bibs of wintering adults in an Ontario population in 1994 and returning adults in 1995, we correlated bib area, perimeter, and amount of white breast feathers interdigitating into the lower edge of the bib (raggedness) with age and sex of birds. Only bib area showed any tendency to be sexually dimorphic; females tended to have smaller bib areas than males. By contrast, raggedness of the bottom of the bib appears to be related to age, rather than sex; raggedness was greater in hatching-year birds than in after-hatching-year birds. Bib morphology of individuals also showed year effects, independent of age. Individual birds from 1994 that were rephotographed in 1995 had more ragged bibs in 1995. Hatching-year birds in 1995 also had more ragged bibs than 1994 hatching-year birds. Consistent differences between years in the degree of bib raggedness suggest that bib morphology could reflect differences in resources at the time of molt.

RELACIÓN DEL TAMAÑO DEL BABERO CON LA EDAD Y EL SEXO EN *POECILE* *ATRICAPILLUS*

Sinopsis.—El tamaño y forma del babero negro en individuos de *Poecile atricapillus* varía entre individuos y puede dar información sobre la edad y el sexo tal y como ocurre en otras especies con insignias de plumaje similar. Correlacionamos el área del babero, el perímetro y la cantidad de plumas blancas del pecho que se interdigitan en el margen inferior del babero (indefinición) con la edad y el sexo de las aves al fotografiar y medir los baberos de adultos invernando en una población en Ontario en 1994 y de adultos retornando en 1995. Tan solo el área del babero mostró una tendencia al dimorfismo sexual: las hembras tendían a tener un babero menor que los machos. Por el contrario, la indefinición del final del babero parece estar relacionado con la edad más que con el sexo: la indefinición fué mayor en aves nacidas en el mismo año que en aves de mayor edad. La morfología del babero de individuos también mostraron efectos anuales independientes de la edad del ave. Individuos del 1994 que se refotografiaron en 1995 tenían baberos más indefinidos en 1995. Aves nacidas en 1995 también tenían baberos más indefinidos que las aves nacidas en 1994. Diferencias consistentes en el grado de indefinición del babero entre los años sugieren que la morfología del babero podría reflejar diferencias en los recursos disponibles al momento de mudar.

Variation in plumage badges among individual birds may convey information on relative fighting ability, thus these signals could be used to assess competitors in order to avoid engaging in costly fights with dominant birds (Rohwer 1975). Associations have been found between individual rank of wintering birds and the degree of dark coloration on their head (Harris' Sparrows, *Zonotrichia querula*; Rohwer 1975, 1977, 1985; Rohwer and Rohwer 1978), breast (Great Tits, *Parus major*; Järvi and Bakken 1984, Järvi et al. 1987) or throat (House Sparrows, *Passer domes-*

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ticus, Møller 1987, 1989). "Cheating" (possessing extensive dark coloration without possessing superior fighting ability) appeared to be controlled through continual probing by other individuals, ensuring congruence between the size of a badge and the motivation to back up the signal. Birds whose badge sizes were experimentally increased suffered increased aggression from flockmates (Rohwer 1977, Järvi et al. 1987, Møller 1987) unless they were also implanted with testosterone, thus simultaneously increasing motivation to reinforce the signal (Rohwer and Rohwer 1978, Järvi et al. 1987).

Despite these early findings, however, recent studies have questioned Rohwer's (1975) suggestion that badge size acts as an absolute predictor of dominance. Associations between badge size and dominance appear to be the result of age and sex differences in plumage characteristics (Watt 1986a,b; Jackson et al. 1988; Wilson 1992). Only when juveniles are manipulated to resemble the plumage of adults does their rank against other juveniles or adults increase (Rohwer 1985, Holberton et al. 1990). However, if variation in plumage accurately reflects age or sex, it may serve as a signal of potential fighting ability when the rival is unfamiliar (Lemel and Wallin 1993). This is especially true if the size of the plumage badge is either partially dependent on access to resources, which also tend to be age, sex, and rank dependent (Balph et al. 1979, Hogstad 1988, Smith 1984) or related to physical condition of the individual (Møller 1989, Veiga 1993, Gustafsson et al. 1995).

We investigated whether plumage variability in the black bibs in Black-capped Chickadees (*Poecile atricapillus*) varies predictably with age and sex. Chickadees begin flocking in the fall, following the onset of the post-breeding molt of adults (July/August) and the first prebasic molt of young birds (August/September) (Smith 1991). Winter flocks usually consist of 2–4 mated pairs, normally an adult pair that bred the previous spring and several pairs of hatching-year birds pairing for the first time (Smith 1991). Dominance hierarchies are established within flocks through aggressive displays. During aggressive encounters in chickadees, the bib of the aggressor bird is prominently directed at the subordinate bird (the *gape*, *bill up*, and *body ruffling* displays; see Smith 1991). However, no formal analysis has determined whether the morphology of the bib varies with age, and previous studies that investigated sex difference in the shape of the bib produced conflicting results (Mosher and Lane 1972, Gochfeld 1977). If characteristics of the bib do covary with age and sex: (1) juveniles may be able to use bib characteristics to distinguish between older birds, especially older, dominant males, and avoid aggressive interactions with them and (2) females may be able to use bib characteristic to assess the age, and thus possible resource holding potential, of males during initial mate choice for pair formation.

METHODS

Adult bib measurement.—Adult chickadees ($n = 108$) were captured at the Queen's University Biology Station, Chaffey's Locks, Ontario (44°3'N,

76°1'W) between January and May 1994 (>90% from 6 Jan.–1 Feb. 1994). This data set was used to analyze relationships between the area and perimeter of the bib in relation to body size, age, and sex. For analyses of age and sex, we used 70 birds from the larger sample, whose sex was determined with confidence using a combination of body measurements (Desrochers 1990) and behavior during the breeding season, and whose age was determined by shape of the outer rectrices (hatching year, HY, versus after hatching year, AHY; Meigs et al. 1983). The numbers of birds in each age and sex category in 1994 were: 21 AHY males, 16 HY males, 16 AHY females, and 17 HY females. This smaller sample constituted approximately 80% of the males and females making up the focal breeding population in the spring of 1994.

We took a standardized photograph of the bib of each bird at time of capture. Chickadees have a single annual molt in the early fall, therefore the winter plumage is retained into the spring (Smith 1991). The bird was held with its bill approximately parallel with the body, with the base of the skull resting on the scapula. In this position, the bib is fully visible, but the feathers are not stretched. All birds were photographed in the same standardized position with an 80 mm lens held approximately 30 cm from the bird. A centimeter ruler was placed beside the bird to give relative scale, and a Canadian Wildlife Service band number was included in each photograph for individual identification.

Using a lightboard, we traced the outline of the photographed bib onto tracing paper or clear acetate. We traced the largest continuous area of black feathers starting and finishing at the base of the bill. The feathers of the bib are dark from base to tip, while breast feathers are dark at the base and white at the tip (pers. obs.). The distinction between the end of the black bib feathers and the white-tipped breast feathers varies between birds. In many individuals, white-tipped breast feathers interdigitate with the lower edge of the bib giving the lower edge a "ragged" appearance (see Mosher and Lane 1972, Gochfeld 1977, Smith 1991) (Fig. 1). We followed the edge of the black feathers excluding any interdigitating white feathers, and also excluding any black feathers that were completely isolated from the bib by white breast feathers.

We scanned traces using Ofoto 2.03 (Light Source Computer Images) and imported the files into CANVAS 3.06 for Macintosh (Deneba Systems, Inc.). Using CANVAS, we adjusted the rulers to compensate for the small differences in scale between photographs. In CANVAS, we retraced the bibs using the polygon tool at a 300% enlargement to minimize measurement error. Using the program's measurement scale, we then calculated the area and perimeter of the bib from the tracings. This technique yields highly repeatable measurements, as calculated using the repeatability index given in Lessells and Boag (1987). We retraced and remeasured the bib photograph of 11 captive males originally measured 2 wk previously, without reference to the original tracing. Bib measurements were highly repeatable for both area and perimeter (area: $r = 0.98$; perimeter: $r = 0.92$). Eleven different captive males photographed twice

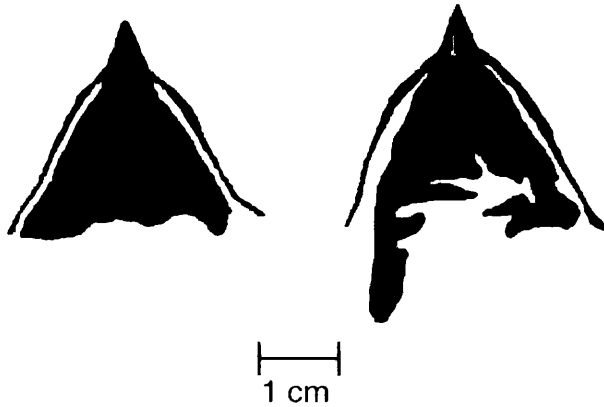


FIGURE 1. Variation in bib morphology among individual Black-capped Chickadees. Traces were prepared from photographs of wintering chickadees in 1994 and 1995. Birds were held with bill parallel with their body axis and base of skull resting on the shoulders in order to photograph the full bib. Birds were identified by legband number and ruler provided scale.

(each letting the bird relax for several minutes between successive photos) also showed high repeatability between bib measurements (area: $r = 0.88$; perimeter: $r = 0.80$).

Analysis of bib morphology.—Bib area and perimeter are positively related ($F_{1,106} = 26.4$, $P = 0.0001$), but area of the bib did not account for a high proportion of the total variance in the perimeter ($R^2 = 0.20$). Although some of this variation is likely attributable to small differences in shape of the bib, much of this variation is likely due to bib raggedness described by Mosher and Lane (1972). When white breast feathers interdigitate the bottom edge of the bib, this increases the perimeter in relation to the area of the bib (Fig. 1). Thus, we included the standardized residuals of the perimeter on area regression (hereafter termed residual perim/area) as an approximate measure of variance in bib morphology attributable to raggedness.

We use the terminology residual perim/area in reporting statistical results to distinguish our quantitative measure from the subjective scoring of Mosher and Lane (1972), but use residual perim/area to approximate raggedness in describing this characteristic of bib morphology in the discussion, so as to compare directly with earlier studies. To ensure that the residual scores did reflect a qualitative measure of raggedness, we asked three biologists naive to the aims of the study to classify 98 photographs of 1994 birds into one of two categories with respect to the lower edge of the bib, ragged or smooth. Scorers were given Figure 1 of Mosher and Lane's (1972) study as an example. In addition, another naive observer was asked to pick from the photographs of birds an example of one bird each with a smooth or ragged bib. These two photographs were also given to the scorers as examples, and were excluded from later analysis. There

was consistency between scorers in classification of most birds (61/98 were assigned to the same category by all three scorers). On average, 72 of the 98 birds were classed into the same categories by any two scorers. In cases where disagreements in classification occurred, the final designation of the bird as ragged or smooth bibbed was based on that agreed by two of the three scorers. Birds that were scored as smooth bibbed had significantly lower residual perim/area scores than birds scored as ragged bibbed (Mann-Whitney Test: $U = 1365$, $n = 33, 65$, $P = 0.027$).

Changes in bib morphology within and between individuals: year effects.—In the winter of 1995 (13 Dec. 1994–9 Jan. 1995), 33 surviving birds photographed the preceding year were rephotographed and bibs remeasured using the same technique described above. The ages of these birds in 1994 were split equally between the two age classes (16 were AHY in 1994, 17 were HY). These data allowed the comparison of changes in bib characteristics of returning birds to determine the consistency of bib morphology with age. In addition, 10 birds (six males, two females, and two birds of unknown sex) who had hatched in the study population in 1994 were photographed during the same period in the winter of 1995 (these constitute a group of 1995 HY birds). To determine whether bib characteristics of juveniles differed between years, HY birds in 1995 were compared to a similar sized group of HY birds in 1994.

Statistical analysis.—We used regressions to compare bib morphology to body size. To test bib area, perimeter, and residual perim/area against age and sex of adults, we used two-factor ANOVAs. Comparison of changes in bib characteristics of birds returning in 1995 were conducted with two-factor repeated measures MANOVAs with age and sex as between-subject factors, and year as the within-subject factor. All analyses were two-tailed.

RESULTS

Bib morphology and body size.—There was no significant relationship between any measure of bib morphology (area, perimeter, or the residual perim/area) and any measure of body size (mass, wing chord, and rectrix) (Table 1). Thus, differences in body size between males and females is unlikely to bias any sex differences found in bib morphology.

The relation of bib morphology with age and sex.—There was a tendency for males to have larger bib areas than females, but there was no significant difference in bib area between age classes, and no interaction between age and sex on bib area (sex: $F_{1,66} = 3.0$, $P = 0.088$; age: $F_{1,66} = 0.025$, $P = 0.88$; age/sex interaction: $F_{1,66} = 0.75$, $P = 0.39$) (Fig. 2a). There was no difference between males and females in bib perimeter, but HY birds had significantly larger bib perimeters than AHY birds (sex: $F_{1,66} = 0.99$, $P = 0.32$; age: $F_{1,66} = 4.38$, $P = 0.04$; age/sex interaction: $F_{1,66} = 0.001$, $P = 0.98$) (Fig. 2b). This difference in perimeters between age classes is supported by the analysis of residual perim/area scores; there was no difference between sexes of the same age class, but older birds had significantly smaller residual perim/area scores (i.e., had less ragged

TABLE 1. Relationship between bib morphology and body size in Black-capped Chickadees as assessed by regression of individual measures of bib against each measure of body size. For a small number of birds, one or more body size datum was missing; these were excluded from analysis giving the slight differences in degrees of freedom between tests.

	Regression			
	R ²	df	F	P
Bib area (cm²)				
vs. mass (g)	0.003	1, 104	0.26	0.61
vs. wing chord (mm)	0.003	1, 103	0.34	0.56
vs. rectrix (mm)	0.004	1, 105	0.46	0.50
Bib perimeter (cm)				
vs. mass (g)	0.002	1, 104	0.17	0.68
vs. wing chord (mm)	0.002	1, 103	0.17	0.68
vs. rectrix (mm)	0.012	1, 105	1.33	0.25
Residual perim/area				
vs. mass (g)	0.005	1, 104	0.55	0.46
vs. wing chord (mm)	0.006	1, 103	0.59	0.44
vs. rectrix (mm)	0.008	1, 105	0.85	0.36

bibs) than young birds (sex: $F_{1,66} = 0.017$, $P = 0.89$; age: $F_{1,66} = 6.38$, $P = 0.014$; age/sex interaction: $F_{1,66} = 0.3$, $P = 0.59$) (Fig. 2c).

Change in bib morphology with age within individuals.—Based on the results presented above, we predicted that as HY birds from 1994 aged to become AHY in 1995, there would be: (1) little change in bib area and (2) a decline in bib perimeters, resulting in (3) a decrease in the residual perim/area scores. Conversely, we predicted (4) little change in all three variables in birds AHY in both 1994 and 1995. We also predicted (5) there would be parallel changes for males and females in the same age categories, as there was little indication that perimeter or residual perim/area was affected by sex.

Contrary to our predictions, however, there were no differences in bib morphology that were attributable to aging from a HY bird to an AHY bird; rather, the differences in bib morphology seemed more attributable to sex differences than age differences. There was a significant decline in bib area between years within individuals; this was primarily attributable to a tendency for bib area to decline more in females than males (Table 2). There was an overall increase in bib perimeter between years within individuals, with a significant effect of the sex of the birds: males returning in 1995 had a larger increase in bib perimeters than females. There was no effect of the age of the bird in 1994 on the differences within individuals in bib perimeter. Finally, there was an overall increase in residual perim/area scores among birds. Once again, there was a marginal effect on the sex of the birds in the difference in residual perim/area scores: males tended to have a larger increase in residual scores between years than females but not significantly so. Age of the birds in 1994 had

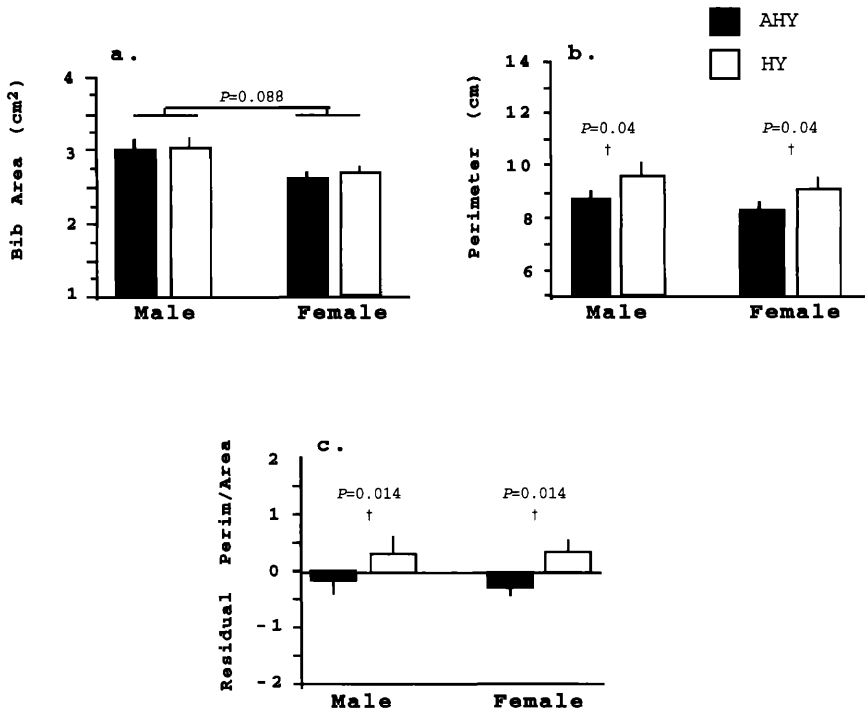


FIGURE 2. Bib area (a), perimeter (b), and residual perim/area scores (c) of wintering chickadees in 1994 were compared between males and females as well as after hatching year and hatching year birds (M/AHY = 21, M/HY = 16, F/AHY = 16, F/HY = 17). Data presented are means \pm SE. Analyses are two-factor ANOVA; bars indicate differences between sexes. † indicates significance between age classes within sex ($P < 0.05$).

no effect on changes in residual perim/area. This suggests that all birds, but particularly males, tended to return in 1995 with more ragged bibs.

Comparison of general bib characteristics between years.—If bib raggedness is related to general condition of the plumage, consistent effects such as the within-individual increase in bib raggedness seen above, could be the result of yearly fluctuation in resources available during the time of molt. If conditions were less favorable during molt for birds wintering in 1995 than 1994, we might also expect HY birds in 1995 to have more ragged bibs than HY birds in 1994. We compared the bibs of the 10 birds that were HY in 1995 to the 17 birds that were HY in 1994 that also returned as AHY in 1995. The latter group was chosen as it represented a similar sized group of birds to the HY birds measured in 1995. In addition, there was no significant difference between this group of HY birds from 1994 that returned ($n = 17$) and other HY birds in 1994 that did not return the following winter ($n = 16$) on any of the three measures of bib characteristics (area: $t = 0.69$, $P = 0.50$; perimeter: $t = 0.73$, $P = 0.47$; residual

TABLE 2. Within-individual changes in bib area, perimeter, and residual perim/area between 1994 and 1995 in 33 Black-capped Chickadees photographed in both years. Analyses are repeated measures MANOVA with differences in each variable between years as the within-subject factor, and differences in the age of birds in 1994 (Hatching year or After hatching year) and sex as between-subject factors that may contribute to between-year differences in bib morphology. Average values are shown as mean \pm SE based on classification of subjects.

Variable	1994	1995	MANOVA	
			<i>F</i>	<i>P</i>
Area (cm ²)				
Within-subject factor				
Overall effect	2.89 \pm 0.11	2.53 \pm 0.075	6.98	0.013
Between-subject factors				
Age 1994			0.74	0.79
HY	2.92 \pm 0.15	2.69 \pm 0.07		
AHY	2.87 \pm 0.16	2.57 \pm 0.14		
Sex			3.18	0.085
M	2.85 \pm 0.14	2.74 \pm 0.09		
F	2.98 \pm 0.16	2.43 \pm 0.13		
Age 1994 * Sex			0	0.99
M/HY	2.85 \pm 0.19	2.78 \pm 0.08		
M/AHY	2.84 \pm 0.23	2.70 \pm 0.17		
F/HY	3.03 \pm 0.27	2.52 \pm 0.10		
F/AHY	2.92 \pm 0.22	2.34 \pm 0.24		
Perimeter (cm)				
Within-subject factor				
Overall affect	9.11 \pm 0.31	10.27 \pm 0.39	5.29	0.03
Between-subject factors				
Age 94			1.09	0.3
HY	9.57 \pm 0.53	10.35 \pm 0.56		
AHY	8.61 \pm 0.28	10.20 \pm 0.57		
Sex			5.22	0.03
M	8.76 \pm 0.39	10.59 \pm 0.50		
F	9.72 \pm 0.49	9.72 \pm 0.65		
Age 94 * Sex			0.001	0.98
M/HY	9.08 \pm 0.66	10.50 \pm 0.74		
M/AHY	8.41 \pm 0.40	10.70 \pm 0.68		
F/HY	10.49 \pm 0.85	10.08 \pm 0.89		
F/AHY	8.95 \pm 0.31	9.36 \pm 1.00		
Residual perim/area				
Within-subject factor				
Overall affect	-0.79 \pm 0.26	0.68 \pm 0.39	12.26	0.002
Between-subject factors				
Age 94			1.6	0.22
HY	-0.34 \pm 0.44	0.69 \pm 0.53		
AHY	-1.26 \pm 0.20	0.67 \pm 0.60		
Sex			3.38	0.076
M	-1.08 \pm 0.32	0.87 \pm 0.52		
F	-0.27 \pm 0.35	0.35 \pm 0.60		
Age 94 * Sex			0.001	0.98
M/HY	-0.77 \pm 0.57	0.73 \pm 0.71		
M/AHY	-1.43 \pm 0.24	1.02 \pm 0.8		
F/HY	0.44 \pm 0.63	0.60 \pm 0.86		
F/AHY	-0.97 \pm 0.36	0.09 \pm 0.91		

perim/area: $t = 0.56$, $P = 0.58$). When comparing the HY birds in 1995 with HY birds in 1994, the 1995 HY birds had smaller bib areas (t -test: $t = 2.6$, $df = 26$, $P = 0.016$) and larger residual perim/area scores ($t = -2.176$, $df = 26$, $P = 0.039$) than the 1994 HY birds. There was no difference in the bib perimeter between the 1994 and 1995 HY birds ($t = -1.059$, $df = 26$, $P = 0.30$).

DISCUSSION

In comparison to after-hatching-year birds, hatching-year chickadees of either sex had larger perimeters (total outline of the bib) and larger residual perim/area scores (more white feathers along the bottom edge). Thus, younger birds tended to have more ragged lower bib margins than older birds. Our results contrast with those of Mosher and Lane (1972), who suggested that raggedness of the bib distinguished males and females, a suggestion that was also disputed by Gochfeld (1977). We found some evidence for sexual dimorphism in bib area, a feature not measured by either Mosher and Lane (1972) or Gochfeld (1977). Bib area tended to be larger in males than females in 1994. This tendency for a sex difference in bib area is not merely a correlate of smaller body size of the female, because there was no association between bib area and any measure of body size. Thus, chickadees appear similar to other species, such as Dark-eyed Juncos (Balph et al. 1979) and Great Tits (Järvi and Bakken 1984, Wilson 1992) in which males have larger plumage badges than females. To determine whether bib morphology is influenced by intersexual selection, aviary studies where females are allowed to pair with novel males with manipulated bibs will be required. In the congeneric Great Tit, females prefer males with wider breast stripes as mates (Norris 1990).

Chickadee bib morphology also appears to indicate age, at least in the larger sample of 1994, with after-hatching-year birds having smaller perimeters and less ragged bibs than hatching-year birds. This age difference in bib morphology is similar to that found in Harris' Sparrows (Watt 1986 a,b; Jackson et al. 1988) and juncos (Holberton et al. 1990). Neither Great Tits nor House Sparrows were found to have badge size vary with age (Järvi and Bakken 1984, Møller 1987, Wilson 1992; cf. Veiga 1993 for House Sparrows). Our results, along with others (e.g., Norris 1990) suggest it may be important to consider additional aspects of badge morphology beyond area, such as perimeter and shape, in testing for age effects.

Age differences in bib morphology may prove to be effective in both intersexual and intrasexual signalling. Perception of age of competitors may prevent young birds from engaging in interactions with older birds that are likely to be dominant, it may be advantageous for females to be able to assess age of unfamiliar, unpaired potential mates.

We had predicted that between-year differences in the bibs of individuals would primarily reflect changes in age classes; individuals undergoing their first adult molt (e.g., going from HY molt to AHY) should show a greater decrease in bib raggedness than individuals going from one AHY

molt to the next. However, the differences that we saw in bib morphology between years were more related to sex than to changes in age. While all birds had significant increases in bib perimeters between 1994 and 1995, males of both age classes in 1994 (HY or AHY) returned with a greater increase than females. As a result, all birds in the winter of 1995, but primarily males, had larger residual perim/area (bibs were more ragged) than they had been the previous winter.

This overall increase in raggedness may be attributable to environmental differences affecting birds, such as the relative amount of resources available at the time of molt. We cannot completely discount subtle differences in measurement between years, although steps were taken to decrease this problem (same photographer, protocol and equipment in both years as well as the same individual tracing and measuring photographs). In addition, the procedure produces highly repeatable results from multiple photos of the same individual taken over a shorter time scale (see above). There is some supporting evidence that differences in bib raggedness between years reflect differences in resources at the time of fall molt. First, the effects of the increase in bib raggedness between years was consistent; the effect was seen across all individuals, though slightly heightened in males. Second, HY birds in the winter of 1995 had smaller bib areas and more ragged bibs than a similar sized sample of HY birds from the winter of 1994. These trends suggest bib morphology could be condition dependent. Captive studies on Carolina Chickadees (*Poecile carolinensis*; Grubb 1991) and European Starlings (*Sturnus vulgaris*; Swaddle and Witter 1994) have suggested that food levels affect the condition of feather development. Swaddle and Witter (1994) found periodic food stress during the fall molt resulted in higher levels of asymmetry in breast feathers. If food availability at the time of molt in chickadees affects bib morphology, the shape and raggedness of the bib may reflect individual condition, as is known to occur in the plumage of Collared Flycatchers, *Ficedula albicollis* (Gustaffsson et al. 1995) and House Sparrows (Møller 1989, Veiga 1993). In order to assess the importance of food availability on bib development, similar experiments of housing chickadees on variable diets are required. By varying food availability or protein levels of the diet during the fall molt, the condition dependence of bib raggedness, and thus its signal potential, could be assessed.

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