WHY ARE WAXWINGS "WAXY"? DELAYED PLUMAGE MATURATION IN THE CEDAR WAXWING

D. JAMES MOUNTJOY[1] AND RALEIGH J. ROBERTSON
Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

ABSTRACT.—Cedar Waxwings (*Bombycilla cedrorum*) often have their secondaries tipped with red waxlike appendages, but a plausible hypothesis for the function of these tips has not been presented. Both males and females may have such tips, but second-year birds normally have none or only a few. This appears to be the first described instance of a passerine species to show distinctive delayed plumage maturation in both sexes. We found that waxwings mated assortatively with respect to the number of tips on the secondaries of the birds. Pairs of older birds (with high tip index scores) tended to nest earlier than younger (low tip index) birds. Older birds also had larger clutch/brood sizes and fledged more young. We suggest that the waxlike tips function as signals of age and status and that some combination of mate choice and competition for mates results in the observed assortative mating. Of the hypotheses proposed to explain the adaptive significance of delayed plumage maturation, two (the female-mimicry and cryptic hypotheses) are not confirmed in the case of the Cedar Waxwing, while the status-signaling hypothesis appears to offer the best explanation for the occurrence of delayed plumage maturation in this species. *Received 6 March 1987, accepted 15 September 1987.*

ALL three members of the family Bombycillidae have red appendages resembling small drops of sealing wax at the tips of their secondaries. These appendages are apparently uncommon in the Japanese Waxwing (*Bombycilla japonica*) but are common in both the Bohemian (*B. garrulus*) and the Cedar (*B. cedrorum*) waxwings. The secondary tips are basically flattened extensions of the feather shafts and are composed of a dorsal, amorphous, pigmented layer over a more structured medullary layer, with both layers being surrounded by a transparent cuticle (Brush and Allen 1963). The red pigment is astaxanthin, a carotenoid pigment that has also been identified in the feathers of other bird species. The precursor for this pigment is probably dietary in origin (Brush and Allen 1963). We will refer to these structures as tips for simplicity.

Although these unique structures have intrigued many ornithologists, few have been able to suggest a possible function for them. Wilson and Bonaparte (1832, cited by Tyler 1950: 80) felt that the tips of the Cedar Waxwing were "intended for preserving the ends, and consequently the vanes, of the quills, from being broken and worn away. . . . The feathers of those birds which are without these appendages are uniformly found ragged on the edges, but smooth and perfect in those on whom the marks are full and numerous." In examining numerous live birds and museum skins, however, we have found no obvious relationship between tips and feather wear. In those few birds where feather wear is obvious the entire plumage is affected, including the primaries, tail, and contour feathers, regardless of whether the secondaries have tips. It also is unlikely that the secondaries would require more protection from wear than the primaries. Most writers, like Coues (1903: 360), simply state "Their use is unknown."

The distribution of waxlike tips among birds of different sex and age classes in the Cedar Waxwing has been difficult to determine because of the general similarity of plumage between males and females and a lack of philopatry, which makes it difficult to follow changes in the plumage of known-age individuals. Some authors indicate that there are no differences between the sexes in the number of tips (e.g. Chapman 1966, Wood 1969), while others have suggested that the birds with the greatest number are usually males (Mearns 1878, cited by Putnam 1949; Dwight 1900; Coues 1903; Tyler 1950). Yunick (1970) examined 255 after-hatching-year (AHY) specimens of known sex and concluded that, although more females than males lacked the tips and more males than fe-

---

[1] Present address: Department of Biology, McGill University, 1205 Dr. Penfield Avenue, Montreal, Quebec H3A 1B1, Canada.

males had maximum counts of these appendages, they were not useful as a sexing criterion.

Presence or absence of these tips may be an indication of the age of the bird. Birds in juvenile plumage may possess tips and apparently mature birds often lack them (Coues 1903), but Chapman (1966) stated that the absence of these appendages was "doubtless an indication of immaturity." Wood (1969) likewise suggested that the presence or absence of tips could be used to separate second-year (SY) from after-second-year (ASY) birds from January to August, even though some young birds have a few small appendages. Yunick (1970) found that about 95% of a large sample of juveniles (n = 326) lacked tips on the secondaries, and that when present they were fewer in number and reduced in size compared with adults. Because the postjuvenile molt (occurring in September and October) replaces only body plumage and not flight feathers or the tail (Dwight 1900), most Cedar Waxwings will lack tips at least until they are about 14 months old. If SY birds acquire a full complement of appendages at the first postnuptial molt, then this feature could be used to separate SY and ASY birds with considerable reliability. No data are available concerning the proportion of birds that develop tips at this stage, and banders have been advised not to use these appendages for aging (Anon. 1980).

Despite the uncertainty concerning exactly when Cedar Waxwings acquire the tips on their secondaries, this is most likely an age-related feature. Most SY birds lack tips, but because a large percentage of AHY waxwings (including SY as well as ASY birds) have them, most, if not all, waxwings must develop them later in life. Therefore, this seems to represent an unusual case of delayed plumage maturation. Among the North American passerines there are at least 38 species in which males do not develop full breeding plumage until their second potential breeding season (Rohwer et al. 1980, Lyon and Montgomerie 1986). In addition, at least in the Tree Swallow (*Tachycineta bicolor*) the female rather than the male does not develop full adult plumage for the first breeding season (Rohwer et al. 1980, Stutchbury 1986). Rohwer et al. (1980) did not include the Cedar Waxwing among the species they designated as having delayed plumage maturation. The species meets the criterion for delayed plumage maturation suggested by Lyon and Montgomerie (1986), namely "any retention of first winter plumage colors that could be used to distinguish most SY males from adult males. . . ." The feature that makes the Cedar Waxwing different from all other species that have been described as possessing delayed plumage maturation is that neither sex acquires full adult plumage in its first breeding season.

We examined the distribution of secondary tips among the different sex and age classes of Cedar Waxwings to clarify the patterns that have been suggested by previous authors. Additionally, we investigated the possibility of differences in relative success at obtaining mates or opportunities to breed for birds with or without a full complement of tips, and looked for differences in time of arrival at breeding sites between age classes that might help to explain any such differences. We also compared breeding success and other reproductive parameters for young and old birds. Finally, we discuss how unusual aspects of the waxwing social system might influence the mechanisms of delayed plumage maturation, and examine the relevance of this species to general theories dealing with the adaptive significance of delayed plumage maturation.

METHODS

Fieldwork was carried out at the Prince Edward Point National Wildlife Area in Prince Edward Co., Ontario, in May-September of 1984 and 1985. Data on the distribution of secondary tips were collected from 162 AHY birds captured with mist nets and from 31 nestlings at Prince Edward Point. Only breeding birds were sexed, using the presence or absence of a brood patch as the distinguishing criterion. In addition, we examined 240 waxwing specimens from the collections of the Royal Ontario Museum and the National Museum of Canada (48 nestlings or juveniles and 192 birds in postjuvenile plumage).

We counted the number of tips on the secondaries of both wings for each individual. Most waxwings had an equal number of tips on each wing, but there frequently were small asymmetries. The tip index score was defined as equal to the total number of secondary tips on both wings except in the case of birds that had at least one very small (less than 1 mm) tip, in which case each small tip contributed 0.5 to the score.

An age distribution for Cedar Waxwings was estimated from recovery data on banded birds supplied by the Canadian Wildlife Service. We used all recoveries of birds banded during their hatching year in Canada and the United States to calculate the proportion of birds that survived to 1 June of their second and subsequent years.

Data on the breeding success of birds with few or many waxlike tips were extracted from the more extensive information gathered while studying the general breeding biology of this species (Mountjoy 1987). Breeding birds in most cases were assigned to tip index categories after being mist-netted and examined, but in a few cases birds were assigned to a category after close examination in the field using 10× binoculars or a spotting scope. First-egg dates for most pairs were determined by back-dating based on known hatching dates or fledging dates and average incubation and nestling periods of 12.5 and 15 days, respectively (Putnam 1949).

RESULTS

Distribution of tips among sex and age classes.—A total of 162 birds in AHY plumage was banded and examined in the field. Half of these birds had no tips at all, and an additional 13% had tip index scores of 5 or less. The remaining 37% had a relatively large number of tips, with tip index scores ranging from 9.5 to 17 (Fig. 1A). The distribution of tip index scores was bimodal, with peaks at 0 and 14 and no birds with scores between 5.5 and 9. A similar pattern was obtained in the examination of 174 museum skins of adult birds in unstreaked plumage (Fig. 1B). Birds with no tips comprised about 49% of this sample, while birds with scores of 6 or less made up an additional 5%. Approximately 45% of the birds were well adorned with waxlike tips, with scores ranging from 10 to 19 and a peak again at 14. Because there are two distinct categories we refer to birds with scores between 0 and 6 as beta birds and birds with scores from 9.5 to 19 as alpha birds. The relative proportions of alpha and beta birds, based on all AHY birds examined in the field and all museum skins with no indication of immaturity in plumage or in the label data, were 0.41 and 0.59, respectively.

Both males and females were well represented in the alpha and beta categories. In one sample of skins of male waxwings the percentages of alpha and beta birds were 53% and 47%, respectively; this is a significantly higher proportion of alpha birds than was found in a sample of skins of female waxwings (Table 1).

Among the skins of nestlings and juveniles examined ($n = 48$), 77% lacked tips completely, while another 17% were in the beta category. A further 4% had tip index scores of 8 and were intermediate between alpha and beta birds, unlike any of the postjuvenile birds. Only one bird was classified as an alpha with a score of 11, although the tips were smaller than those typical of older birds. In addition, in 31 nestlings examined in the field most lacked well-developed tips, although a number had fine hairlike projections from the feather shaft that were not considered in the determination of tip index scores. Distinct waxlike tips were present on 35% of the nestlings. Six of the nestlings (19%) possessed only a few small tips (tip index scores ranging from 0.5 to 6), while another 13% fell into the intermediate range, with tip index scores of 7 or 8. Only 1 nestling (3%) was classified as an alpha bird.

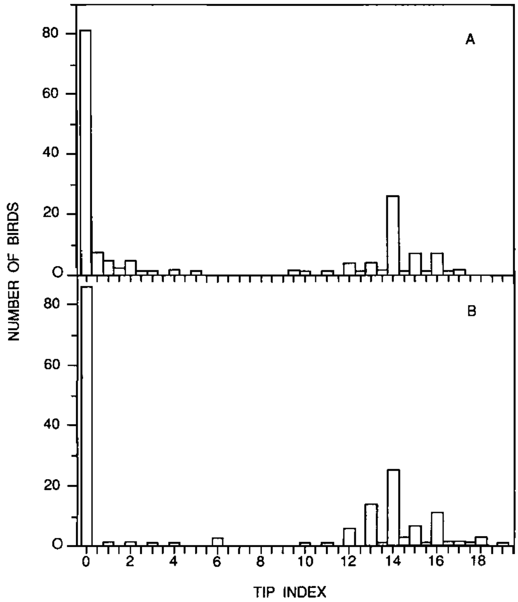


Fig. 1. Distribution of tip index scores (see text) for after-hatching-year waxwings (A) captured at Prince Edward Point and (B) examined as specimens at the Royal Ontario Museum and the National Museum of Canada.

Among the museum skins that were in unstreaked plumage, 18 specimens had incompletely ossified skulls or were simply labeled as immatures, and were presumed to be HY or SY birds. Sixteen of the skins (89%) were in the beta category, a significantly higher proportion than expected among birds in unstreaked plumage overall ($G_{adj.} = 4.14$, $P = 0.042$). The other two specimens of presumed SY birds had tip index scores of 14 and 16.

Overall, when all nestlings and skins of HY or SY birds were considered, only 4% fell in the alpha category, indicating that young wax-

TABLE 1. Specimens of male and female waxwings in the alpha and beta categories. The higher proportion of alpha birds among the males was significantly different from the females ($G_{adj.} = 4.86$, $P = 0.027$). Specimens from the collections of the Royal Ontario Museum and the National Museum of Canada.

	Males	Females
Number of alpha birds	42	27
Number of beta birds	37	49

TABLE 2. Numbers of alpha and beta waxwings captured before and after the median banding date of spring migrants. The trend for a higher proportion of alpha birds to be captured before the median date was significant in 1985 ($G_{adj.} = 3.98$, $P = 0.046$), but not in 1984 ($G_{adj.} = 0.17$, $P = 0.69$) or when both years were combined ($G_{adj.} = 0.94$, $P = 0.33$).

	1984		1985		Combined	
	Alpha	Beta	Alpha	Beta	Alpha	Beta
Before median	16	14	7	10	23	24
After median	8	9	0	5	8	14

wings rarely have a large number of tips. Therefore, the great majority of alpha birds must be in at least their third year. Some nestlings have a few tips, and it is likely that all birds will fall in the alpha category after the first replacement of their flight feathers in the autumn of their second year. We tested this hypothesis indirectly by comparing the proportion of beta and alpha birds banded in the field during late May and early June with the proportion of SY and ASY birds expected to be present in the population at that time of year. The expected proportions of SY and ASY birds were determined from data on recoveries of birds banded as nestlings or juveniles. Of 46 birds that survived at least until the end of May in their second calendar year, 27 died before the next June, and 10, 7, 1, and 1 birds survived an additional 1-4 years, respectively. We calculated that at the beginning of June the population should consist of 59.7% SY birds and 40.3% ASY birds. These proportions do not differ significantly from the 61.7% beta birds and 38.3% alpha birds among the 107 birds we banded at that time of year ($G_{adj.} = 0.070$, $P = 0.791$).

Arrival times of alpha and beta waxwings.—Banding was not begun early enough to capture the earliest returning migrants, but 107 waxwings were caught in late May and early June over the 2 yr. These birds are believed to be mostly migrants in transit, as only one individual subsequently nested in the study area. Some alpha and beta birds were captured from the same flocks on the first banding days of each season, but there was a slight trend for alpha birds to be captured early in the spring banding period (Table 2). This trend was significant statistically in 1985, but not in 1984 or when data from the 2 yr were combined (no significant year effect was found in a multidimensional contingency analysis, thus allowing the data to be pooled).

Relative success in obtaining mates.—Some waxwings might be excluded from breeding if the sex ratio is imbalanced. It is difficult to determine the sex ratio of the local waxwing population, in part because most of the banding effort during the breeding period was directed toward capturing specific individuals at their nests.

The proportions of alpha and beta waxwings among individuals that bred did not differ from the overall proportions of these two classes among all of the AHY birds examined in that year. In 1984 beta birds comprised 61% of all AHYs examined and 58% (11 of 19) of known breeders. In 1985 beta birds comprised 66% of the AHY waxwings and 62% (13 of 21) of the breeding birds captured. Overall, there was no indication of a difference in the proportions of alpha and beta waxwings that might have been excluded from breeding ($G_{adj.} = 0.034$, $P = 0.85$).

Alpha and beta waxwings did not mate randomly, however, as most pairs were composed of two birds belonging to the same tip index category (Table 3). In both years this assortative mating by tip category was significant, and when the two years were combined the probability of achieving this result by random mating was reduced to less than 0.001.

Breeding success of alpha and beta pairs.—Alpha pairs tended to start nesting earlier than beta pairs. The average first-egg date for alpha pairs was 10 days earlier than for beta pairs (1984 and 1985 combined), but this difference was not significant ($t = 1.54$, df = 14, $0.1 < P < 0.2$). When females from mixed pairs were included in the analysis, the difference in the number of alpha and beta females starting clutches before or after the median date was significant (Table 4).

Many of the nests observed were not discov-

TABLE 3. Assortative mating by tip index category in Cedar Waxwings. The number of alpha and beta females mated with either an alpha or a beta male is shown. The assortative mating was significant in both years (1984: $G_{adj.} = 3.95, P = 0.047$; 1985: $G_{adj.} = 6.440, P = 0.011$) and highly significant overall ($G_{adj.} = 11.766, P = 0.0006$).

	Males					
	1984		1985		Combined	
	Alpha	Beta	Alpha	Beta	Alpha	Beta
Females						
Alpha	4	0	3	0	7	0
Beta	2	3	1	6	3	9

TABLE 4. Numbers of alpha and beta female waxwings that laid their first eggs before or after the median date. Alpha females initiated laying earlier than beta females in 1985 ($G_{adj.} = 4.62, P = 0.032$) and for both years combined ($G_{adj.} = 3.89, P = 0.049$), but not in 1984 ($G_{adj.} = 0.449, P = 0.503$).

	1984		1985		Combined	
	Alpha	Beta	Alpha	Beta	Alpha	Beta
Before median	2	2	3	2	5	4
After median	1	3	0	5	1	8

ered until the nestling stage, and some other nests were not checked for contents upon initial discovery to avoid causing desertion; hence, initial clutch sizes are not known for many nests. A comparison of the earliest known contents indicated that beta pairs had significantly smaller clutch or brood sizes than alpha pairs (Table 5).

Alpha pairs also fledged significantly more young than beta pairs (Table 5). This held after we excluded 4 nests of beta waxwings that failed because of human disturbance or that lost all of their contents to predators. This difference probably was due primarily to lower clutch sizes for beta pairs, but beta birds also fledged a slightly lower proportion of the earliest known contents of the nest, and the only observed case of a nestling dying in the nest involved a beta pair.

DISCUSSION

Distribution of tips.—We support the suggestion of Yunick (1970) that the number of tips present on Cedar Waxwings is correlated with the age of the bird. Our results differ somewhat in that we found a higher percentage of young birds with secondary tips than he reported. Yunick found that 95% of the 326 juvenile-plumaged birds banded in New York and 91% of 52 juvenile skins examined completely lacked tips. They were absent in only 65–77% of the immature birds we examined. Some juveniles with only a few small tips may have been overlooked in Yunick's study as the data were collected during the operation of a weekend-manned banding station. Overall, the results are similar; Yunick also reported a very small percentage of juveniles with a substantial number of tips, and a few individuals that probably were in the intermediate category. It is not entirely clear why some juveniles had tip index scores in the intermediate range while no AHY birds did. A few of the small tips found on young birds may have been lost through abrasion without the loss being detected.

The slightly lower proportion of alpha individuals among females is consistent with a similar trend in Yunick's (1970) data. This trend might indicate a lower survival rate for female waxwings. Female-biased mortality has been postulated to occur frequently in species with delayed plumage maturation (Rohwer et al. 1980, Lyon and Montgomerie 1986). A shortage of females could account for the presence of a few mixed pairs composed of alpha males and beta females.

Pair formation and assortative mating.—Young (beta) and old (alpha) birds apparently associate together in migrant flocks and arrive together in the breeding area; thus, segregation by age cannot account for the observed age-assortative mating. Males do not appear to defend territories (Mountjoy 1987) and thus do not benefit from early arrival to claim an area of high-quality habitat. Courtship activity is initiated within the flock, often several months before breeding (Putnam 1949), and it is a prolonged process. Individuals attempting to obtain a mate must therefore remain with the flock. In such a system, where birds choose mates on the basis of individual rather than territory quality, we might expect characters that advertise the quality of the individual to be strongly selected for (Lyon and Montgomerie 1986). The waxlike tips of Cedar Waxwings indicate the age of the bird and appear to be such a character.

TABLE 5. Comparison of reproductive measures of beta and alpha pairs.

		Beta pairs		Alpha pairs			
Reproductive measure	Year	$\bar{x}$	(n)	$\bar{x}$	(n)	t	P
Earliest known contents	1984	4.33	(3)	5.25	(4)	2.255	$0.05 < P < 0.1$
	1985	2.50	(4)	4.67	(3)	3.277	<0.05
No. of young fledged/nest	1984	4.5	(2)	5.0	(4)	0.730	>0.5
	1985	2.0	(3)	4.33	(3)	3.500	<0.05

The assortative mating by tip category suggests that waxwings may exercise mate choice based on the plumage of potential mates. Assortative mating can also result from intrasexual competition or incidental effects (Arak 1983). Unfortunately, the assortative mating observed in waxwings cannot be ascribed fully to the influence of either mate choice or intrasexual competition. One or both of these factors may be operating. Direct field observations of pair formation and experimental manipulations are unavailable. Nonetheless, certain aspects of this system suggest that mate choice is likely to be important in waxwings. Few individuals are excluded from breeding, and there is no indication that polygamy ever occurs. Most individuals probably will be equally successful in obtaining a mate, and intense competition for a mate *per se* should not be frequent. It may be possible, as well, to draw an inference from the nature of the signal waxwings use. Most species that use status signals in an aggressive context have signals that are easily visible in face-to-face confrontations. Examples are the breast stripe in Great Tits (*Parus major;* Jarvi and Bakken 1984), throat color in Harris' Sparrows (*Zonotrichia querula;* Rohwer 1975), and crown stripes in White-crowned Sparrows (*Z. leucophrys;* Parsons and Baptista 1980). In contrast, the tips on the secondaries of waxwings would not be easily visible in typical threat posture but should be clearly visible to both members of the pair during courtship hopping (Putnam 1949). This does not necessarily imply that the waxy tips have no function in agonistic encounters, but if a signal has a dual function, then the secondary function might be slightly compromised to provide a clear message in its primary context. Such evidence is far from conclusive, but it suggests that mate choice might be a factor in the evolution of feather appendages in Cedar Waxwings.

The benefits of choosing an older mate are implied by the higher breeding success of alpha pairs. For example, the tendency for alpha pairs to begin nesting earlier than beta pairs may give these pairs the chance to raise two broods in a season. The main reason for the higher breeding success seemed to be the larger clutches laid by older (alpha) females. Young females in many species have smaller clutch sizes or lay smaller eggs than older birds, and have lower fledging success (Crawford 1977, Curio 1983). Females are often considered to be the more discriminating sex with regard to mate choice because of their greater reproductive investment (Trivers 1972). In monogamous species such as the Cedar Waxwing, female quality can influence the male's reproductive success. Therefore, we might expect males to be choosy in selecting mates if opportunities for mating are limited. Nonetheless, females also might do significantly better if they obtain older mates. Male waxwings provide most of the females' food during incubation, and feed nestlings more frequently than do females (Mountjoy 1987). Older males may provide better care for offspring or provide food more efficiently to the female, and therefore reduce the costs incurred by the female and potentially influence egg mass or clutch size (Nisbet 1977).

Cedar Waxwings and delayed plumage maturation.—The Cedar Waxwing is unique among the passerine species ascribed to possess delayed plumage maturation. This is the only known species in which ASY birds of both sexes have a distinctly different plumage from SY birds in the breeding season. Further, the great majority of the species that have been described as possessing delayed plumage maturation are strongly dichromatic (Rohwer et al. 1980). This may in part be due to the ease of identifying subadult plumages when the plumage of the adult male is bright and highly distinctive. The species with conspicuously colored males often show strong territorial behavior, and males may arrive on the breeding grounds before females (Rohwer et al. 1980). In waxwings, however, competition for mates and mate choice occur in flocks where individuals are in close proximity. A less conspicuous, but distinctive, signal may be as effective as the bright colors in other species, but not have the disadvantage of making the bird more vulnerable to predators.

Previous studies of delayed plumage maturation have focused attention on the fact that many subadults are excluded completely from breeding. The subadult plumage was considered part of a strategy designed to increase the probability of obtaining a breeding opportunity. Most subadult Cedar Waxwings apparently breed, and the plumage of an individual may more often be important in influencing with whom a bird mates rather than determining whether the bird will mate at all.

Two of the hypotheses that have been proposed to explain delayed plumage maturation in other species are inappropriate for the Cedar Waxwing. The female-mimicry hypothesis (Rohwer et al. 1980) holds that subadult males mimic females to avoid confrontations with resident adult males until they can acquire sufficient site dominance to defend a territory successfully. Cedar Waxwings do not defend a clearly defined territory, and both male and female waxwings have a subadult plumage that does not resemble the plumage of adult females. The cryptic hypothesis (Selander 1972, Procter-Gray and Holmes 1981) posits that subadults invest less reproductive effort in their first breeding season and attempt to reduce their costs by adopting a less conspicuous plumage. Although the poor reproductive performance observed in beta pairs may be indicative of some degree of reproductive restraint (Curio 1983), most young birds invest a considerable effort in breeding attempts, and the absence of feather tips does not make an individual less conspicuous to predators.

It is more difficult to reject the winter-adaptation hypothesis (Rohwer et al. 1983) as a possible explanation for the delayed plumage maturation in Cedar Waxwings. This hypothesis suggests that dull plumages in young passerine birds are selected for by unspecified factors that operate during the winter. Any effect of these plumages observed during the breeding season is a nonadaptive consequence of winter adaptations. Cedar Waxwings (unlike some species exhibiting delayed plumage maturation) do not undergo a prenuptial molt; if the lack of tips was favored during the winter, then young birds might be constrained from acquiring these appendages, and the winter-adaptation hypothesis would apply. Lyon and Montgomerie (1986) argued that the winter-adaptation hypothesis is unlikely to provide a general explanation of delayed plumage maturation because it cannot explain the correlation obtained between delayed plumage maturation and the defense of type-B nesting territories. For the evolution of delayed plumage maturation in Cedar Waxwings to be favored solely by factors operating outside the breeding season, the benefits would have to offset any disadvantages encountered during the breeding season. These disadvantages possibly include exclusion of some young males from breeding and lower breeding success in beta pairs. How young birds would benefit sufficiently from delayed plumage maturation during the winter to compensate for the large disadvantages suffered during the breeding season without some adaptive value in the breeding season is unclear. In winter Cedar Waxwings associate in large flocks and feed on persistent fruits, descending en masse on a localized source of food and leaving the vicinity when the supply is exhausted (Tyler 1950). The lack of fighting among birds in foraging flocks has been noted (e.g. Allen 1930, Tyler 1950), and we have never noted overt aggression over food. In fact, flocks have greater success than individuals in gaining access to defended fruit sources (Moore 1977), so older birds may benefit from tolerating young birds in nonbreeding flocks.

The hypothesis that best explains delayed plumage maturation in the Cedar Waxwing is the status-signaling hypothesis (Lyon and Montgomerie 1986). This hypothesis assumes that females select mates on the basis of plumage color. The dull plumage of SY males is viewed as a reliable signal of subordinance that advertises their lower intrinsic resource-holding potential. Young birds are less attractive to females and therefore less threatening to adult males. Young birds probably benefit from this honest signaling of status because they receive less aggression from the adults. In a species that forms pairs within flocks, this would allow young birds to remain within the flock and possibly obtain mates if there is a sufficient number of potential mates. It also reduces the costs of direct competition in contests that younger birds are unlikely to win.

The status-signaling hypothesis must be generalized to take into account the fact that both sexes of Cedar Waxwings show delayed plumage maturation. As pointed out by Lyon and Montgomerie (1986), the status-signaling hypothesis differs little from the concept of status signaling proposed by Rohwer (1975), and it is appropriate to consider the hypothesis as a specific example of the general phenomenon of status signaling. Status-signaling systems operate during the nonbreeding season in a number of sexually monomorphic species (Rohwer 1975, Parsons and Baptista 1980, Jarvi and Bakken 1984), and other sexually monomorphic species in addition to the Cedar Waxwing most likely will be shown to use status signals during the breeding season.

ACKNOWLEDGMENTS

R. D. Montgomerie, P. T. Boag, and F. Cooke were very helpful with their comments through the course of this study. We also thank RJR's lab and two anonymous reviewers for their comments. We are grateful to Helene Levesque and the Canadian Wildlife Service for permission to work at Prince Edward Point National Wildlife Refuge and for supplying excellent accommodations for the 1985 field season. The Banding Office of the Canadian Wildlife Service supplied banding recovery data. The staff of the Royal Ontario Museum and the National Museum of Canada kindly provided access to their collections. Stephen Maxwell, Darlene Parsons, and Cathy Christie supplied valuable assistance in the field. This study was supported by the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED

ALLEN, A. A. 1930. Cherry bird—the Cedar Waxwing. Bird-lore 32: 298-307.

ANONYMOUS. 1980. North American bird banding techniques, vol. II. Ottawa, Ontario, Can. Wildl. Serv.

ARAK, A. 1983. Male-male competition and mate choice in anuran amphibians. Pp. 181-210 *in* Mate choice (P. Bateson, Ed.). Cambridge, England, Cambridge Univ. Press.

BRUSH, A. H., & K. ALLEN. 1963. Astaxanthin in the Cedar Waxwing. Science 142: 47-48.

CHAPMAN, F. M. 1966. Handbook of birds of eastern North America. New York, Dover Publ.

COUES, E. 1903. Key to North American birds. Boston, Massachusetts, Dana Estes and Co.

CRAWFORD, R. D. 1977. Breeding biology of year-old and older Red-winged and Yellow-headed blackbirds. Wilson Bull. 89: 73-80.

CURIO, E. 1983. Why do young birds reproduce less well? Ibis 125: 400-404.

DWIGHT, J., JR. 1900. The sequence of plumages and molts of the passerine birds of New York. Annals New York Acad. Sci. 13: 73-360.

JARVI, T., & M. BAKKEN. 1984. The function of the variation in the breast stripe of the Great Tit (*Parus major*). Anim. Behav. 32: 590-596.

LYON, B. E., & R. D. MONTGOMERIE. 1986. Delayed plumage maturation in passerine birds: reliable signalling by subordinate males? Evolution 40: 605-615.

MEARNS, E. A. 1878. A description of unusually developed individuals of three species, and remarks on uncommon plumages in several others, taken near West Point, N.Y. Bull. Nuttall Ornithol. Club 3: 69-72.

MOORE, F. R. 1977. Flocking behaviour and territorial competitors. Anim. Behav. 25: 1063-1065.

MOUNTJOY, D. J. 1987. Behavioural ecology of the Cedar Waxwing during the breeding season. Unpublished M.Sc. thesis, Kingston, Ontario, Queen's Univ.

NISBET, I. C. T. 1977. Courtship feeding and clutch size in Common Terns *Sterna hirundo*. Pp. 101-109 *in* Evolutionary ecology, biology and environment, vol. 2 (B. Stonehouse and C. Perrins, Eds.). London, Macmillan Press.

PARSONS, J., & L. F. BAPTISTA. 1980. Crown color and dominance in the White-crowned Sparrow. Auk 97: 807-815.

PROCTER-GRAY, E., & R. T. HOLMES. 1981. Adaptive significance of delayed attainment of plumage in male American Redstarts: tests of two hypotheses. Evolution 35: 742-751.

PUTNAM, L. S. 1949. The life history of the Cedar Waxwing. Wilson Bull. 61: 141-182.

ROHWER, S. 1975. The social significance of avian winter plumage variability. Evolution 29: 593-610.

———, S. D. FRETWELL, & D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. Am. Nat. 115: 400-437.

———, W. P. KLEIN JR., & S. HEARD. 1983. Delayed plumage maturation and the presumed prealternate molt in American Redstarts. Wilson Bull. 95: 199-208.

SELANDER, R. K. 1972. Sexual selection and dimorphism in birds. Pp. 180-230 *in* Sexual selection and the descent of man, 1871-1971 (B. G. Campbell, Ed.). Chicago, Aldine.

STUTCHBURY, B. J. 1986. Reproductive tactics of subadult female Tree Swallows (*Tachycineta bicolor*). Unpublished M.Sc. thesis, Kingston, Ontario, Queen's Univ.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136-179 *in* Sexual selection and the descent of man, 1871-1971 (B. G. Campbell, Ed.). Chicago, Aldine.

TYLER, W. M. 1950. *Bombycilla cedrorum* (Vieillot), Cedar Waxwing. Pp. 79–102 *in* Life histories of North American wagtails, shrikes, vireos and their allies (A. C. Bent, Ed.). U.S. Natl. Mus. Bull. 197.

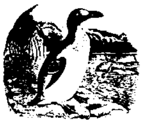
WILSON, A., & C. L. BONAPARTE. 1832. American ornithology.

WOOD, M. 1969. A bird-bander's guide to the determination of age and sex of selected species. University Park, Pennsylvania State Univ.

YUNICK, R. P. 1970. An examination of certain aging and sexing criteria for the Cedar Waxwing (*Bombycilla cedrorum*). Bird-Banding 41: 291–299.

---

100 Years Ago in The Auk



From "General Notes" (1888, Auk 5: 119):

"**What Birds indicate Proximity to Water, and at what Distance?**—Mr. William Lloyd, in his explorations in the arid region of Western Texas, has made some highly important observations, the results of which cannot fail to be of the utmost value to travellers on our southwestern plains, where water is scarce and difficult to find. Mr. Lloyd writes: 'During the past summer, I have been investigating an important question which occurred to me about four years ago, namely, What birds indicate the presence of water in their neighborhood? Of course any statement on the subject should be proved by a number of facts, based on experiments in different localities. Three times this summer I have camped from simply seeing certain birds, and on hunting for water have found it in each case. As certainties I can give the following species, with the greatest distance at which each occurs from water.

Cardinal	1 mile.
Warblers (including Chat)	1 mile.
Vireos	2 miles.
Mockingbirds	2½ to 3½ miles.
Blue Grosbeak	2½ to 3½ miles.
Orchard Oriole	3 miles.
Bullock's Oriole	3 miles.
Nonpareil	3 miles.
Carolina Dove	3 to 5 miles.
Black-capped Titmouse	4 miles.
Texas Cardinal	6 miles.

" 'This only applies to summer, and will not hold in winter or during migrations. I have been constructing this list since the summer of 1883; and also have particularly noted what birds drank, and how often, in Dec.-Jan., 1884-1885; Nov.-Dec., 1885; and Jan., 1886.'—C. HART MERRIAM, *Washington, D. C.*