MOLT AND PLUMAGE VARIATION BY AGE AND SEX IN THE CALIFORNIA AND BLACK-TAILED GNATCATCHERS

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Despite much recent interest in the systematics and demography of the California Gnatcatcher (*Polioptila californica*) (Atwood 1988, 1991, Phillips 1991, Mellink and Rea 1994), the molts and plumages of this species have not been described in detail, though treated briefly by Swarth (1902), Ridgway (1904), Woods (1949), and Dunn and Garrett (1987). According to these references, the first prebasic molt is partial, including the body feathers but not the flight feathers (here defined as the primaries, primary coverts, secondaries, and rectrices), subsequent prebasic molts are complete, and a limited prealternate molt includes the crown feathers, at least in males. Females and most but not all basic-plumaged males lack substantial black in the crown, whereas alternate-plumaged males have black crowns. Though females are browner on the back, flanks, and undertail coverts than males, most published sources report that the sexes are only subtly differentiated, if at all. Except for the juvenal plumage, no plumage differences by age have been confirmed.

Long ago, Swarth (1902) pointed out that basic-plumaged male but not female California Gnatcatchers have short black streaks over their eyes. This character, in the California and/or Black-tailed (*P. melanura*) Gnatcatcher, has been cited by some subsequent references (Woods 1949, Dunn and Garrett 1987, Howell 1987) but overlooked by others (Ridgway 1904, Oberholser 1974, Pyle et al. 1987). Swarth's hypotheses that this black streak is found in males of first basic as well as definitive basic plumage and that basic-plumaged birds with black in the crown are older males have not been confirmed. Dunn and Garrett (1987) further suggested that females have less white in the outer rectrices than do males, and Howell (1987) indicated that basic-plumaged male Black-tailed Gnatcatchers sometimes have a black mask. None of these sources, however, presented any specific data supporting their observations. A critical examination of the California and Black-tailed Gnatcatchers' plumages and molts is thus appropriate.

METHODS

Pyle examined all specimens of the California Gnatcatcher at the San Diego Natural History Museum (SDNHM; n = 115), Natural History Museum of Los Angeles County (LACM; n = 96), California Academy of Sciences (CAS; n = 48), Museum of Vertebrate Zoology, University of California (MVZ; n = 236), and Western Foundation of Vertebrate Zoology (WFVZ; n = 12) and all specimens of the Black-tailed Gnatcatcher at SDNHM, CAS, MVZ, and WFVZ (n = 212). The examination covered all

subspecies of both gnatcatchers from all parts of their ranges (see Atwood 1988, Phillips 1991, Mellink and Rea 1994).

On each specimen Pyle noted color and condition of the flight feathers, color of the nape and back, color of the lower underparts, and occurrence, location, and percentage of black or blackish in the crown. Our findings allowed us to determine the age, as first-year or older (hereafter "adult"), of almost all specimens. We found 21 (3.1%) postjuvenile specimens that we believe to have been missexed. This proportion of missexed specimens is typical of passerines in North American specimen collections (Parkes 1989, Pyle pers. obs.). Terminology of molts and plumages follows Humphrey and Parkes (1959).

Unitt prepared as study skins 40 specimens of the California Gnatcatcher collected by Eric Mellink in northwestern Baja California in January, February, and December 1991, the specimens on which the description of *P. c. atwoodi* was largely based (Mellink and Rea 1994). He described the extent of molt of each specimen on its label. These specimens constitute the basis of our analysis of the California Gnatcatcher's prealternate molt.

RESULTS AND DISCUSSION

Molt

Examination of prepared specimens confirmed most of what has been published on molt in gnatcatchers, and indicated that the extent of molts is similar in both species. The prebasic molt extends from late July to September. The first prebasic molt includes all lesser and median coverts, all or most greater coverts, up to five consecutive inner secondaries (including the tertials), and zero to all six pairs of rectrices. Twenty first-year (October–January) specimens at CAS and MVZ were examined specifically for extent of molt. Of these, 14 had replaced all the greater coverts; the remaining six had retained one to three juvenal outer coverts. The mean number of inner secondaries replaced was 2.8 (range 0–5); only one bird had not replaced at least one tertial. The mean number of rectrices replaced was 2.4, with eight specimens retaining all juvenal rectrices, six having replaced just the central pair, and two having replaced all six pairs.

Fifty-four specimens had been collected during their adult prebasic molt, and, except for the possible retention of a few primary coverts in some birds (see below), this molt appears complete.

The prealternate molt of the California Gnatcatcher is more extensive than previous literature suggests. Of the 35 specimens collected by Mellink between 16 January and 27 February, 30 were growing at least one new feather on the body. In 28, the molt included feathers other than the crown, and in 26, enough feathers were being replaced that counting the growing feathers individually was impractical. The 21 specimens collected between 16 and 30 January included six that were not molting at all and nine that were replacing only the crown, chin, and/or five or fewer contour feathers elsewhere on the body. The remaining six of this subset were replacing most of the crown, throat, upper breast, back, and scapulars. In none did the molt include the belly, and in only one did it extend to the rump. In two collected on 7 February

the molt included the crown, back, rump, and throat but not the lower breast or belly. By contrast, of the 12 collected from 19 to 27 February, four were molting all tracts of contour feathers, including the belly, and the other eight were molting at least some part of the body posterior of the neck. One of the 12 was replacing the innermost secondaries on both wings.

None of the five specimens collected from 6 to 8 December was molting. It appears from our examinations that gnatcatchers do not have a presupplemental molt as in some other passerines (Thompson and Leu 1994).

From these observations, we suggest the following as the normal course of prealternate molt in the California Gnatcatcher. In mid or late January the molt begins on the crown and chin. From there it spreads posteriorly, though not uniformly, but eventually it encompasses all or almost all of the contour feathers. Of the contour feathers, only those on the belly are possibly not replaced by all individuals. None of the wing and tail feathers are replaced except for the innermost secondaries (tertials) in a few individuals. This was corroborated by older specimens as well: of 143 alternate-plumaged birds at CAS and MVZ, 11% of first-year birds and 24% of adults had replaced from one to three inner secondaries. In a more intensively examined sample of 40 specimens in alternate plumage, 20 in their first spring and 20 older adults, 35% had replaced one or two inner greater coverts and three specimens (one first-year and two older adults) had replaced one or two central rectrices. The proportions of birds with replaced feathers and numbers of renewed feathers were roughly equal in the two age classes.

The molt extends through the end of February, and in some individuals may overlap the beginning of the breeding season: a male collected on 7 February had the testes enlarging, and a female collected on 27 February, still growing a few forehead, chin, nape, and back feathers, had the largest ova enlarging with yolk and was developing a brood patch. Between the sexes, no difference in molt is evident. The 25 January/February females include four not molting, four molting all tracts of contour feathers, and the rest representing stages in between. The 10 males range from one not molting to two replacing the crown, neck, back, throat, upper breast, and scapulars. Inner secondaries had been replaced in a similar proportion of both female and male specimens examined.

Plumage Variation by Sex

Except for juveniles (see below), both California and Black-tailed Gnatcatchers are easily sexed at any time of year. Specimen examination confirms that all males in alternate plumage have black crowns, all males in both first basic and adult basic plumage have a distinct blackish streak above the eye (Figure 1A, B), and that all females in all plumages typically lack black or dusky in the crown. First-year males appear to have, on average, less of this streak than adults (Figure 1A, B), but the age groups overlap in this feature. In addition to this black streak, varying proportions of basic-plumaged adult males retain some blackish in the crown or forehead (Figure 1C), which can be used for sexing. Among males, this feature varies with age (see below).

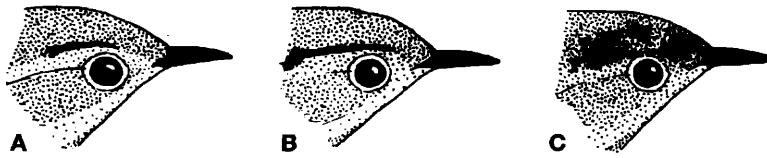

Figure 1. Head patterns of basic-plumaged male California and Black-tailed gnatcatchers. First-year birds (A) have smaller black streaks above the eye than adults (B), but there is overlap between age classes. Some, but not all, basic-plumaged adult males also have a variable proportion of black in the crown (C). Females lack black in the head.

We also confirmed that, in both species, females have more brown in the backs than males. In females, the brown of the back contrasts with the gray crown, whereas in males the crown and back are virtually concolorous, having, at most, a light brownish wash to both the back and the nape. In spring, both sexes have grayer backs than in fall, possibly because of greater wear while the birds are nesting. This sex-specific difference reaches its maximum in the northern populations of the California Gnatcatcher, *californica* and *atwoodi*, in which there is no overlap between females and males (compare figures 3 and 5 in Mellink and Rea 1994). In *pontilis* and *margaritae*, and in the Black-tailed Gnatcatcher, this distinction is less pronounced, especially in spring. On any given date, the sexes can be reliably distinguished by upperpart color, although the brownest males in fall may overlap with the grayest females in spring.

The sexual differences in the color of the flanks and undertail coverts are less pronounced than that of the back. Although there is slight overlap between the buffiest males and the whitest females, even in *californica* and *atwoodi*, this feature could be used as a secondary aid in sexing. We could not confirm that males have more white in the outer rectrices than females (Dunn and Garrett 1987). Any average age/sex-related differences in this character is largely masked by individual and wear-related variation. Of 169 basic-plumaged male specimens examined, only two adult California Gnatcatchers (MVZ 39279 and MVZ 39282, both collected in Claremont, California), had black in the auriculars (i.e., a "mask") as described by Howell (1987). This feature appears to be rare or anomalous, a conclusion now concurred with by Howell (pers. comm.), who has seen only two Black-tailed Gnatcatchers in Mexico with black in the auriculars.

Age Determination

Forty-one juveniles were in the collections we studied, 34 of which had sex designations on the labels. In juvenal plumage, both males and females are washed pale brown over the crown and nape, as previously described (Oberholser 1974, Pyle et al. 1987). Juvenile males tend to have heads less brownish than those of juvenile females, but this difference is slight and probably not useful for sexing single individuals in the field. Juvenile males with at least one black feather behind the eye, presumably renewed first basic feathers, were collected as early as 14 June (MVZ 59736); such birds

could be reliably sexed males. On the other hand, juveniles without black behind the eye, sexed as males, were collected as late as 28 July (MVZ 3250), indicating that juvenile females probably should not be sexed by the lack of a black eye streak until at least mid-August.

We found several criteria that, when combined, can be used to age all male and most female gnatcatchers. Because the first prebasic molt does not include most of the flight feathers, differences in color and abrasion result between low-quality juvenal feathers, grown in the nest, and higher-quality adult feathers, replaced in the late summer. These differences become more pronounced with feather age, so that by spring, the juvenal flight feathers of one-year-old birds are very faded and abraded in comparison to those of adults. If a first-year bird has replaced some inner secondaries or rectrices during its first prebasic molt, the two generations of feathers will contrast.

The most useful age criterion appears to be the color and condition of the outer six or more primary coverts (Figure 2). In fall, juvenal primary coverts are narrow, pointed, and brownish black with a thin edge of gray or brown, whereas those of the adult plumage are broader, more truncate, and duskier

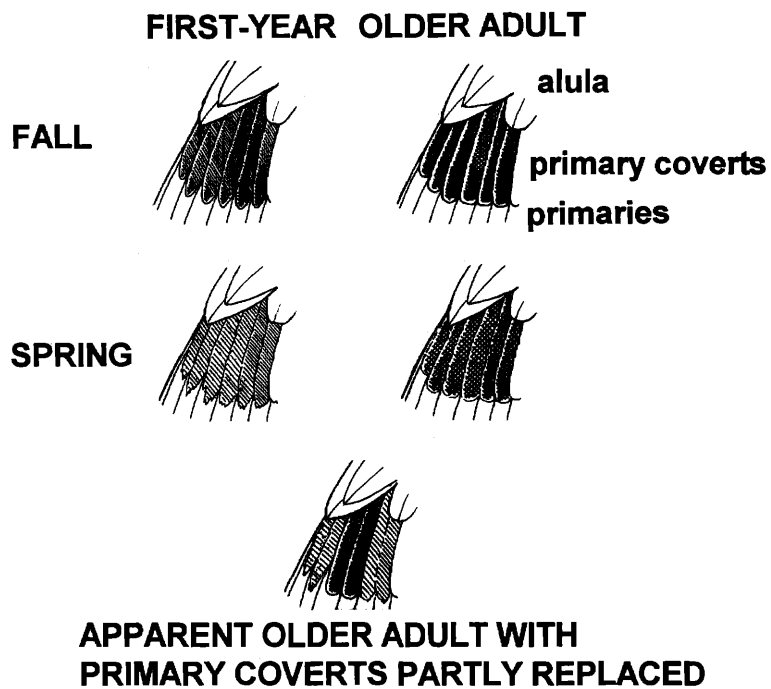

Figure 2. Primary-covert wear and color patterns by age in the California and Black-tailed gnatcatchers. In fall, first-year birds have narrow coverts with thin gray edging, which quickly wears off, leaving the coverts brown and abraded by spring. Adult coverts are broader, with broader gray edging in fall, wearing to thinner gray edging by spring.

centered with broader and fresher gray (male) or brownish-gray (female) edging. The color of the edging typically matches that of the back, as varying by taxon and sex, and tends to be thinner or less distinct in females than in males. By spring, the coverts of first-year birds have lost all traces of edging and are very brown and abraded, while those of adults are brownish black with thinner edging, resembling juvenal coverts in fall. At both seasons these retained juvenal primary coverts (and on some birds the outer one to three greater coverts) contrast in wear with the replaced first basic greater coverts (see Jenni and Winkler 1994 and Pyle 1997a,b for full treatments of these contrasts and their use in age determination in passerines). The primary coverts of adult females may lose the edging in spring (during incubation?) and can be difficult to distinguish from the retained juvenal coverts of first-year birds. Otherwise, the condition of the primary coverts can be used to age most gnatcatchers.

Specimen examination confirmed the suggestion by Pyle et al. (1987) that rectrix shape and condition are not as useful in determining the age of gnatcatchers as in other passerines, including kinglets. (This tends to be true of all passerines with long, graduated tails and rounded rectrices.) Nevertheless, the juvenal rectrices of first-year gnatcatchers in spring tend to be browner and more abraded at the tip than those of adults, sufficiently so that in comparison with a series of specimens the age class of most birds was evident, in agreement with that specified by their primary coverts. Since many individuals replace at least the central pair of rectrices and most replace at least one inner secondary during their first prebasic molt, the contrast between fresher adult feathers and more abraded juvenal feathers is useful in age determination. Note that these contrasts indicate first-year birds only from September through January, as the variability in the extent of prealternate molt means that both age classes may show them in alternate plumage. Because a few individuals replace all rectrices during the first prebasic molt, a uniformly fresh tail does not specify an adult, though a comparatively worn tail does specify a first-year bird. First-year birds that replace the entire tail invariably replace at least the three tertials and so can be aged by contrasts among the inner secondaries.

At least 29 adult gnatcatchers, past their second prebasic molt, had what appeared to be two generations of primary coverts. Contrastingly newer coverts included the second, third, and/or fourth feathers from the outside (Figure 2), and these patterns were either symmetrical in both wings or differed by one feather. Replacement patterns did not correspond with that of the primaries, these being uniformly worn in all cases. These birds, collected between 12 October and 30 May, represented both sexes and all subspecies examined. Examples include SDNHM 13790 (*P. c. margaritae*, collected 22 October), LACM 12775 (*P. c. californica*, 29 November), CAS 41770 (*P. m. lucida*, 3 February), and MVZ 3726 (*P. c. californica*, 13 April).

The contrast between new and old coverts was easier to detect in fresh fall specimens than in worn spring ones and in males than in females, so we may have missed some birds, particularly spring females, with this pattern. Accounting for this, we estimate that 5-10% of adult-plumaged birds had partly replaced primary coverts. The older coverts do not seem as brown or worn as juvenal coverts are in spring, so it appears that this contrast does not

result from an incomplete second prebasic molt, as in woodpeckers (Pyle and Howell 1995). The most logical explanation is that the replacement of newer feathers during the adult prebasic molt had been suspended, resulting in the slight contrast with the feathers replaced earlier. A similar pattern was noted in a small proportion of adult House Finches (*Carpodacus mexicanus*) by Michener and Michener (1940). More study is needed of this interesting replacement pattern.

As mentioned above, some basic-plumaged male Black-tailed and California gnatcatchers have black or blackish in the crown besides the small eye streak (Figure 1C). Using the condition of flight feathers (especially primary coverts) to assign age classes, we found that black in the crown occurs in some (but not all) adult males but not in first-year males (n = 47), confirming Swarth's (1902) conjecture that black in the crown might be found in "old" males only.

In the California Gnatcatcher, blackish in the crown (additional to the streak behind the eye) occurred in 64 of 89 (72%) males in adult basic plumage collected from September through January. The amount of black in the crown ranged from one feather (1%) to 70%; the mean was 14% of all 89 specimens and 20% of birds that had blackish. Fewer male Black-tailed Gnatcatchers in adult basic plumage had blackish in the crown additional to the eye streak (16 of 41; 39%), and the amount of blackish averaged less (4% of all 41 and 11% of those that had blackish). These proportions of black in the crown appear to be similar among subspecies of both species, with a consistent difference between the two species.

In basic-plumaged males with black crowns, the black tends to be flatter and duller than the glossy black of the alternate plumage. Thus, basic-plumaged males of the California and Black-tailed gnatcatchers with blackish in the crowns (Figure 1C) are past their second prebasic molt and can be aged as adults, whereas those without black in the crown, however large the black streak above the eye, should be aged only by the flight feathers. Birds in late January and February need to be checked for molt in the crown, as some first-year birds are growing black alternate crown feathers at this time.

Males in first alternate plumage appear to have duller crowns than adults, on average, sometimes with a few grayish feathers in an otherwise fully black crown, but this difference is slight and not useful on its own for determining the age of single individuals.

The age classes of birds are best determined with a synthesis of all characters. Shape, pattern, and wear of the primary coverts (Figure 2) and outer greater coverts, combined with crown color (Figure 1; especially in *californica*) and color, wear, and contrasts of the rectrices, should reveal the age of almost all male and most female gnatcatchers. Characters of a few birds may be contradictory, e.g., LACM 22888, a male collected on 7 December, which had 20% black (stain?) in the crown but flight feathers resembling those of first-year birds. It is also possible that some very old females might obtain male characteristics, e.g., black in the crown, as occurs rarely in other passerines. Birds showing contradictory features should not be aged or sexed by plumage. Pyle (1997b) summarized age determination of gnatcatchers and other passerines by these criteria.

Molt, Age, and Sex in the Blue-gray Gnatcatcher

Cursory examination of 390 specimens of the Blue-gray Gnatcatcher (*P. caerulea*) indicates that this species' molts resemble those of the California and Black-tailed gnatcatchers. A higher proportion (63%) of alternate-plumaged Blue-gray Gnatcatchers had replaced inner secondaries during the prealternate molt. Most basic-plumaged males do not have black on the forehead and are indistinguishable from females by head plumage; however, females are browner on the back than males, especially in western populations (*P. c. obscura*), and this is probably more useful for sexing than is generally recognized (Pyle et al. 1987, Ellison 1992). Otherwise, molt patterns (including partial replacement of primary coverts in some birds) and criteria for age and sex determinations appear to be similar to those of California and Black-tailed Gnatcatchers.

SUMMARY

Juvenile California and Black-tailed Gnatcatchers are easily distinguished from adult birds by their loose-textured plumage. The sexes of juveniles resemble each other closely, both having a pale brown wash to the upperparts, though males may average slightly grayer on the head and nape than females.

During the first prebasic molt (August–September) the birds replace all of their contour feathers, up to five inner secondaries, and no to all rectrices, but none of their primaries or primary coverts. In the basic plumage, the females are readily distinguished by their browner backs, flanks, and undertail coverts, the difference from males varying by taxon, reaching its greatest in the darkest subspecies, *P. c. californica*. In first basic plumage all males have a small black streak above the eye but none have black on the rest of the crown.

During the prealternate molt (January–March) the birds replace all of their contour feathers (except possibly the belly in some individuals) but none of their primaries or primary coverts. Some birds replace up to three inner secondaries on each wing and, very rarely, the central one or two pairs of rectrices. The alternate plumage may be slightly grayer than the basic plumage, but it wears and fades rapidly since the birds begin nesting as soon as they acquire it. A few one-year-old males may have one or more gray feathers in the otherwise black crown but most attain fully black crowns.

During the adult prebasic molt (late July–September) the birds replace their entire plumage. A few individuals may retain up to three primary coverts for an unknown period. Again, all males have a small black streak above the eye, and some (more in the California Gnatcatcher, fewer in the Black-tailed) have varying numbers of dull black feathers on the rest of the crown.

The contour feathers of the first basic and first alternate plumages are similar to those of the adult basic and adult alternate plumages. But the retention of more worn and faded juvenal flight feathers, especially the primary coverts, allows almost all one-year-old birds to be distinguished until their second prebasic molt. First-year birds have browner primary coverts

with narrow pale edges that wear away quickly; adults have duskier coverts with broader edges that persist in many males and some females through the spring.

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