Have you ever noticed how tattered adult Ruby-throated Hummingbirds look in mid-summer? During fall migration, why don't adult females retain the "nest mark" so conspicuous during the breeding season? And why do body feathers of adults look so fresh during fall migration, considering that, by this time of the year, those feathers should be approximately seven to eight months old?

The Alternate Plumage of the Ruby-throated Hummingbird

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All photos are from the authors' home in St. Gabriel, Iberville Parish, Louisiana. All photos are by © Donna L. Dittmann.

We have designed our yard to be attractive to birds and wildlife, with particular emphasis on hummingbirds. It took a few years to build up our "clientele," but our feeders and flowers now attract large numbers of Ruby-throated Hummingbirds. During spring migration, the first northbound adult males usually appear in early March, and the first females show up by mid-March. Numbers peak in pulses during the second and third weeks of April, when "in-view-at-once" counts at our front porch feeder array can exceed 60 individuals.

Ruby-throated Hummingbirds nest in older second-growth deciduous hardwood forests—in our yard and vicinity, for example. Breeding activity is underway here by mid-March, and by early May we regard counts of 20–40 as representing local breeders, not migrants. Following a modest dip in late May, average counts level off to 20–30 through late June. Sometimes seen as early as mid-May, youngsters tend to be inconspicuous because initially they prefer to visit flowers; they don't become common at our feeders until late June.

We suspect that our breeding females produce two broods per season, as reported by Robinson et al. (1996). We base this assumption on both appearance and behavior: We have observed females suspected of being "ready to lay" (Fig. 1) or collecting nest material as late as mid-August. By early fall, it becomes impossible to distinguish local breeders and their offspring from southbound migrants. Feeder counts increase during August, and the largest numbers pass through in waves during September, when counts of 70–80+ are not uncommon; numbers fluctuate greatly during September (and between years), with accumulation of individuals between cold fronts and an exodus during favorable migration conditions following a front.

Fall counts drop off quickly during October, by which time adults are uncommon; this trend is summarized in Fig. 2. Occasional stragglers linger into early November. Ruby-throats also appear during the winter, and in recent years, we have usually had one or more known wintering individuals from December to April or even into early May. Adults and immatures that have spent the winter can usually be differentiated until early spring by diagnostic plumage and molt features.

Studying Summer Molt: Methods

Published accounts indicate that hummingbirds undergo a single complete molt per year, which for Ruby-throats occurs on the wintering grounds, after fall migration (Baltosser 1995, Robinson et al. 1996, Pyle 1997). Baltosser (1995) stated that Ruby-throated Hum-

Full content for this article is available online <aba.org/birding/v41n5p35w1.pdf>. Online content includes an additional 13 pages of text, 12 large-format photographs, 4 graphs, 2 sidebars, glossary of terms, and literature cited.

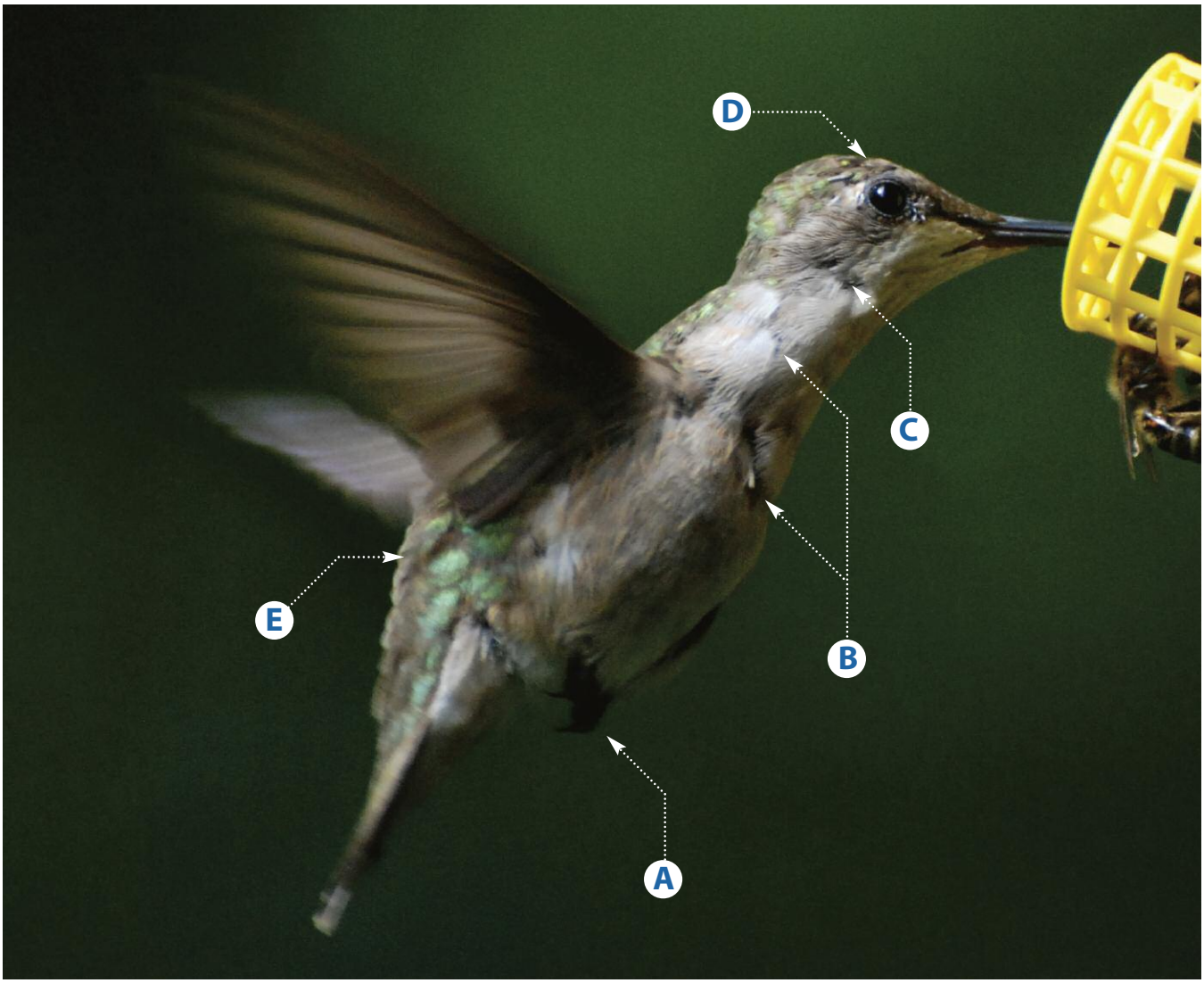
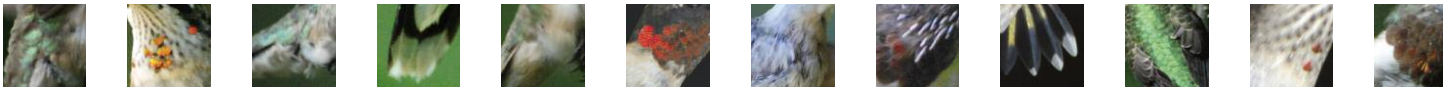


Fig. 1. This **adult female,** photographed 15 July 2007, is likely nearly ready to lay an egg. Although we can't be 100% certain without in-hand examination, this bird clearly has a fat, distended belly **(A),** suggesting the presence of a shelled egg in the oviduct, which causes the abdomen and vent to be thrust outward. Note that this individual looks particularly thin-necked; missing feathers contribute to this appearance.

This "skinny" appearance is in contrast to a bird with pre-migratory fat; on such birds, subcutaneous body fat is deposited around the entire body but most heavily in the furcular region (neck and upper breast), resulting in a conspicuous bulge or roll. Because it is mid-July, the bird in this image has probably already raised one brood. Note that this bird is molting; with close inspection, at least seven sheathed feathers are visible **(B, C, D).** Numerous other feathers are missing, and, although the camera did not freeze motion, the rough, brownish appearance of the lower back **(E)** suggests that molt may also be in progress in this region.



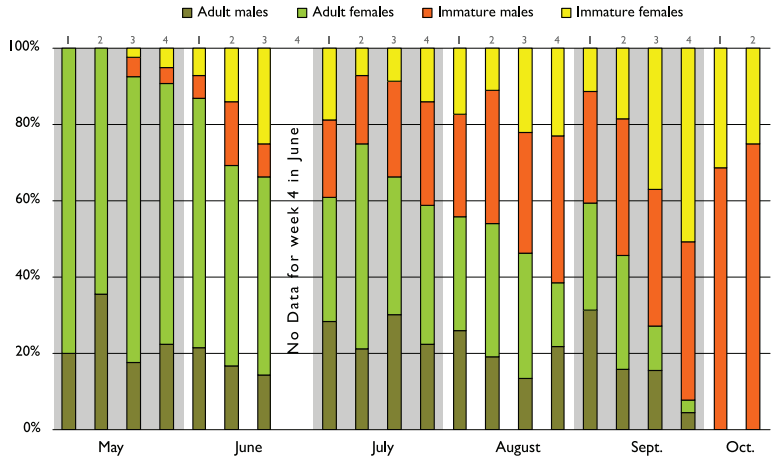


Fig. 2. Shown here is the relative percentage by age and sex of Ruby-throated Hummingbirds present at feeders between the first week of May and second week of October. Data are derived from the photographic study described in the main text of the article; no photographs were obtained during the fourth week of June. *Graph © by Kei Sochi.*

mingbirds "migrate to winter quarters in worn plumage and then undergo a complete annual molt." A number of years ago, however, we began to pay closer attention to our summering population and noticed that a high percentage of individuals were obviously in *active body molt*. Summer molt has not gone totally unnoticed; for example, Robinson et al. (1996) state, "Prebasic body molt may begin on breeding grounds late June (RRS), late August (hatch year female, C.W. Thompson, pers. comm.), Sep or Oct." Also, the phenomenon has been discussed <museum.lsu.edu/~remsen/HUMNETf/molt.html> and illustrated <hiltonpond.org/ThisWeek060822.html> at least anecdotally on the internet. However, body molt observed during the late summer has generally been interpreted as the unusually early onset of a single prolonged prebasic molt that is completed on the wintering grounds.

Our extensive observations of Ruby-throats suggest otherwise. We have discovered that molt during summer and early fall is much more extensive than has been previously reported, both in terms of the number of molting individuals and (at least in adults) the replacement of *a large percentage* (perhaps all) of the body plumage, excluding the flight feathers of the wings and tail. Interestingly, the extensive bird collection at the Louisiana State University Museum of Natural Science has only one (!) Louisiana breeding-season specimen, and it is an adult male with heavy body molt. Thus, in the absence of representative series of specimens, we attempted to document and roughly quantify this summer molt phenomenon in 2006 (summer–fall) and 2007 (spring–fall) with photographs of birds at feeders.

One or two feeders were chosen from an array of 12 (or more) hanging on our front porch (Fig. 3), and hummingbirds were digiscoped (in 2006 with a Nikon Coolpix 5700) or photographed (in 2007 with a Nikon D80 with a Nikkor 70–300 mm lens) as they fed. Ventral and side views (see Fig. 4) were selected for objective comparison of individuals, because sheathed feathers are more conspicuous on the underparts and it is easier to capture such angles at a feeder. One

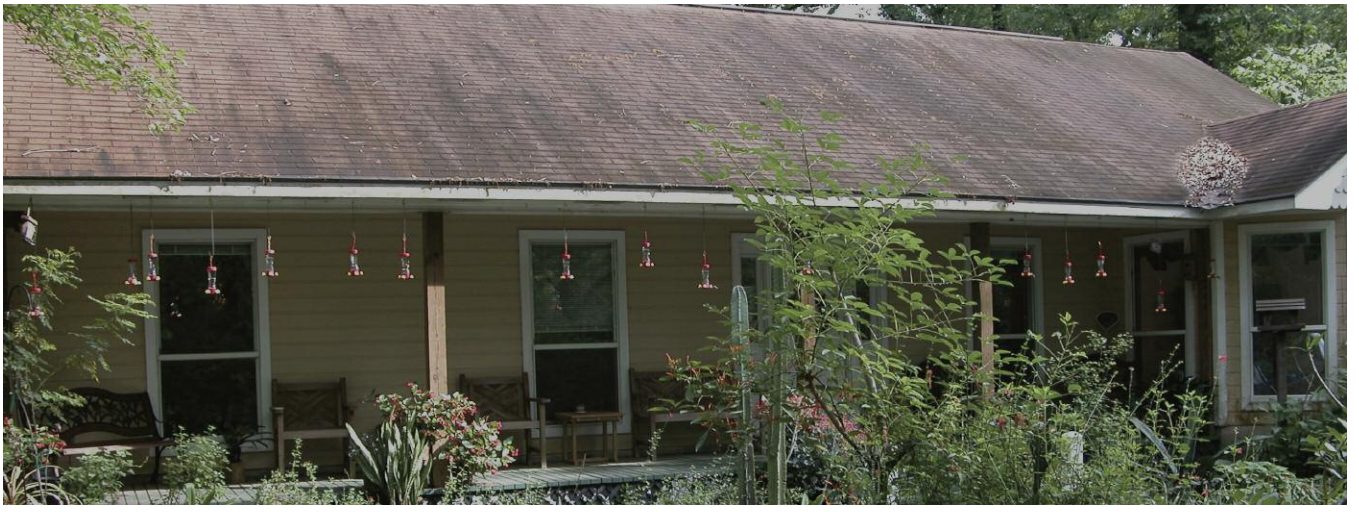


Fig. 3. The study site is a feeder array on the authors' front porch in St. Gabriel, Iberville Parish, Louisiana. Their house is located on three acres of second-growth deciduous forest, approximately 60–80 years old, dominated by water oak, pecan, and hackberry. The garden around the house and the understory vegetation are managed for hummingbirds. The typical "summer" (mid-March–mid-October) feeder array consists of 10–25 feeders, depending on use.

to six photographs were taken per individual, depending on how long a bird used the feeder. Photo sessions ranged from as little as 13 minutes to two hours, with most in the 30–45-minute range, depending on feeding activity, weather, lighting, the photographer's schedule, and her ability to tolerate humidity and mosquitoes.

Due to such variation, there was no attempt at daily standardization (numbers per time of day, etc.). Besides, the primary goal was simply to obtain decent sample sizes of photographed individuals over the course of late spring and summer in order to assess the extent and timing of molt in the local breeding population. Assuming random feeder use by age and sex classes, our photographs documented a sample of birds using particular feeders on a given day. Arrangement of the feeder array, removal of feeder perches, large numbers of competing birds, and proximity of the photographer generally discouraged territorial individuals and reduced skewing of photo sampling.

Some recognizably well-marked individuals (for example, a female with several white remiges and rectrices) would tend to visit the same one or two feeders on any particular day, but such birds did not guard particular feeders or consistently use the same feeders on different days. During review of photographs, some uniquely patterned individuals were detected more than once during a single photo shoot; these individuals were counted only once per day. Because of these known examples, we assumed some duplication of some other individuals, but we believe this duplication too low to influence the overall patterns (see sidebar, p. 35-w13). Usable photographs (adequately portraying age, sex, and plumage) were obtained of 2,543 Ruby-throated Hummingbirds. In 2006, photos of approximately 574 individuals were taken on 18 days during the period 8 July–1 October, plus 21 October. In 2007, photos were taken of approximately 1,969 birds on 49 days during the period 4 May–12 October, plus 6 April. Data were consolidated into four-week intervals. No photos were obtained during the fourth week of June (Fig. 2).

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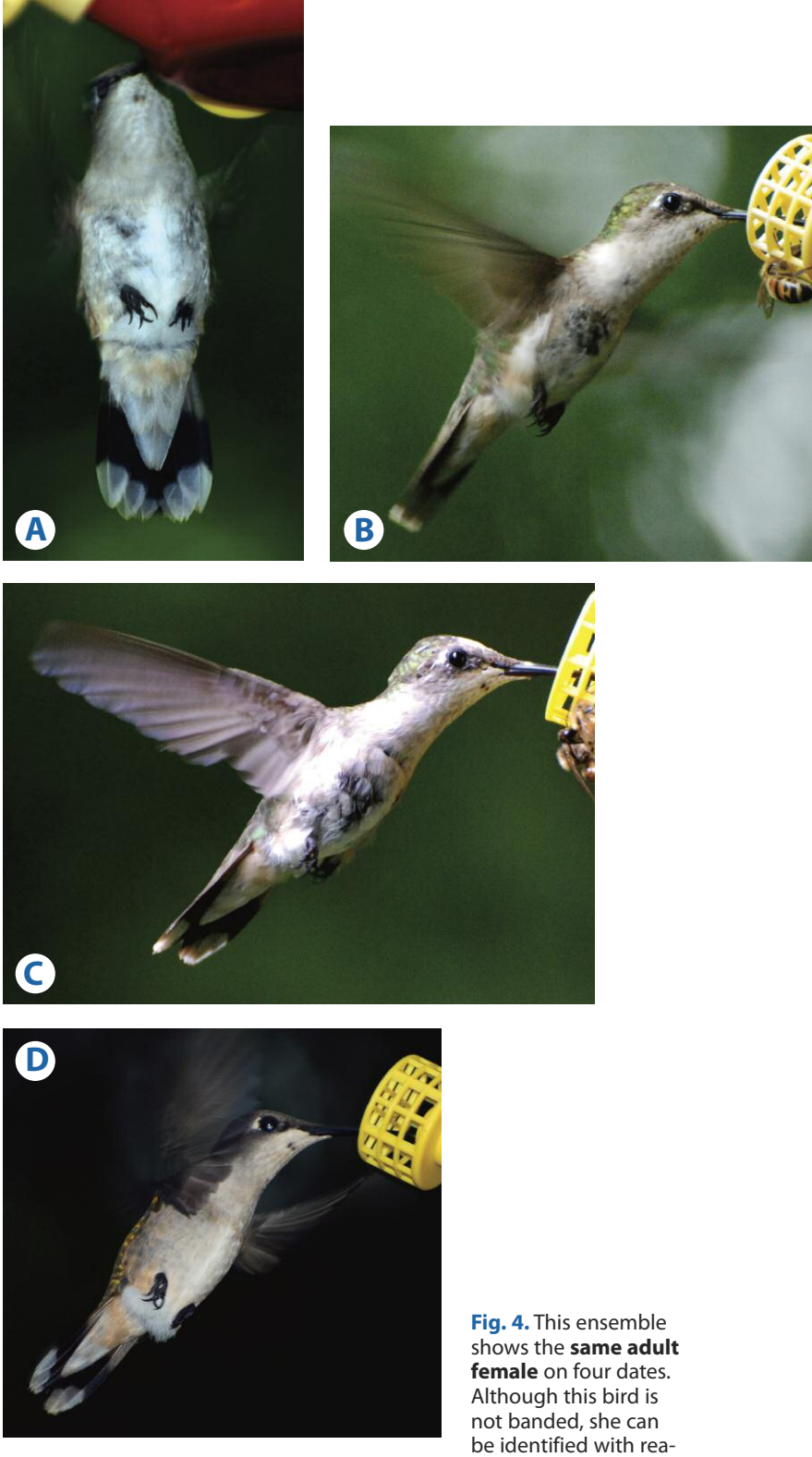

Fig. 4. This ensemble shows the **same adult female** on four dates. Although this bird is not banded, she can be identified with reasonable certainty by her unique plumage: Two dark throat spots identify this particular individual. On 26 May 2007 **(A),** she shows slight wear on the underparts, likely caused by feather abrasion during nest building and incubation of her first brood; the dark blotch is created by exposed dark feather bases, the result of missing or damaged feathers.

On 17 June 2007 **(B),** she shows greater wear and more missing or damaged feathers. By 28 July 2007 **(C),** her underparts are worn and tattered, most likely from abrasion during incubation of a second brood; her "nest mark" is conspicuous. Also note at least three sheathed feathers on the crown, indicating that body molt is now underway. By 1 September 2007 **(D),** the bird lacks a nest mark (no more holes or missing feathers). Her plumage is fresh; the feathers have buffy edges, and the femoral tufts are fluffy. Her worn and tattered feathers on the underparts have clearly been replaced prior to departure for the wintering grounds.

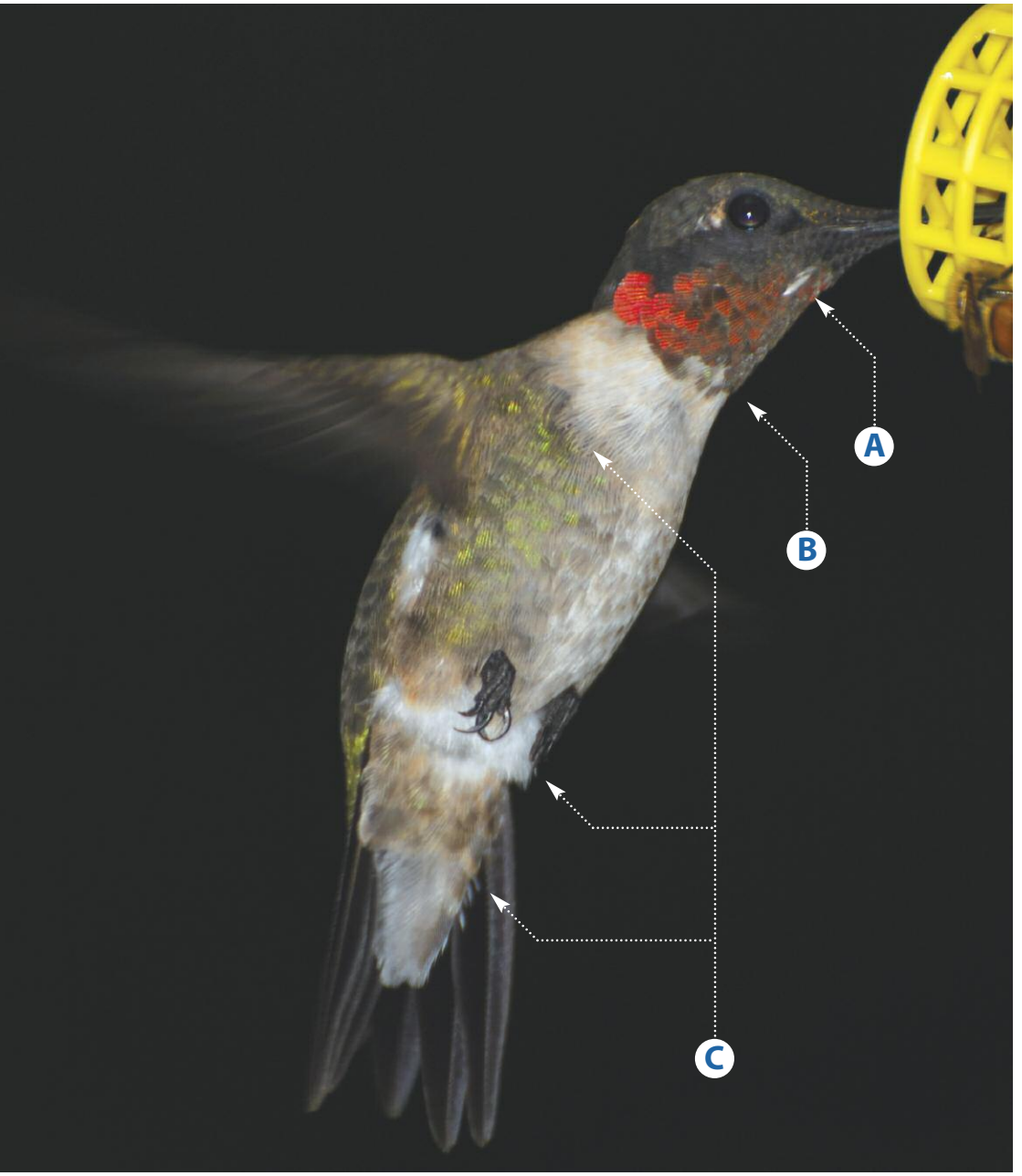

Fig. 5. Adult males are characterized by an iridescent red gorget, green barred sides, and a black forked tail. This male, photographed 1 August 2007, is nearly finished with his summer molt. A few gorget feathers are still sheathed **(A),** but some are missing **(B).** The fresh body feathers **(C)** of the throat, breast, sides, and undertail coverts have distinctive peach-colored edges, which will quickly fade to white with wear. The fluffy femoral tufts are visible.

Determination by photographs of age and sex is straightforward for adult males (Fig. 5). The age-diagnostic pale-edged secondaries of juveniles are not visible on hovering birds, however, so adult females (Fig. 6) were distinguished from juveniles (Fig. 7) by the lack of a scaly appearance to the crown, face, and upperparts, and, to a certain extent, by feather wear, especially on the underparts and rectrices (worn and blunt-tipped R3 and R4; see Fig. 4d). Juveniles are easy to recognize by their fresh flight feathers and scaly looking body feathers, but individuals from early broods can become quite worn by late summer. Moreover, offspring from early broods could potentially linger until early September. At this time, their juvenile* feathers could be more than three months old, making separation of worn juveniles from adult females more problematic. If iridescent gorget spots are absent, juvenile males tend to have dark-centered throat feathers, giving them a "five-o'clock shadow" look, which helps separate juvenile males from most adult females.

Additional characters can be used to separate juvenile males—especially those with plainer whitish throats (Fig. 8)—from juvenile females. These include the less-rounded shape of R5, the smaller

**Astute readers may wonder if the word "juvenal" (instead of "juvenile") should appear here. See pp. 14–15 in this issue of* Birding *for an explanation. —Editor*

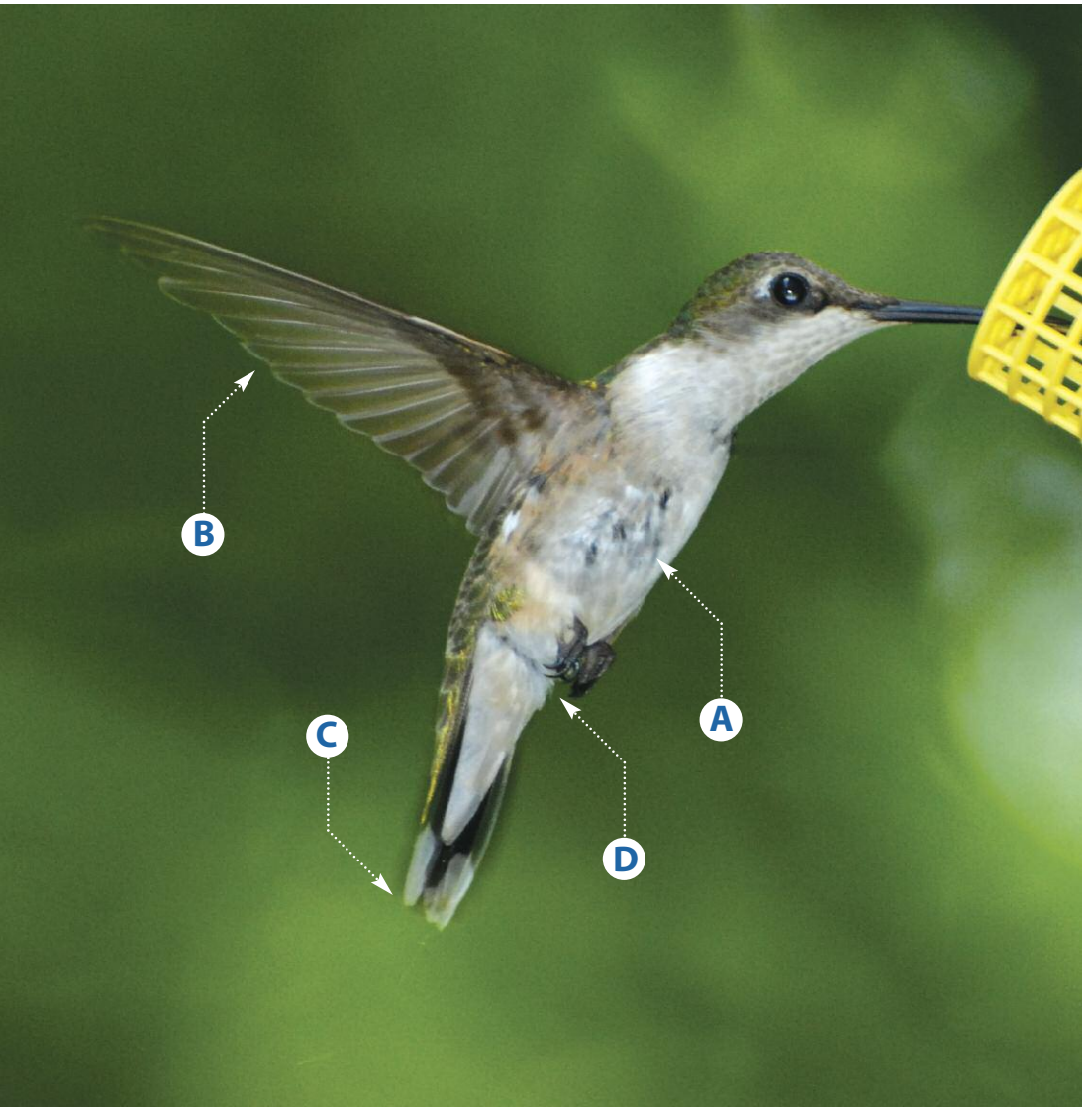

Fig. 6. Adult females are distinguished from juveniles by a number of characters, the most conspicuous being a "nest mark" **(A)** that is present prior to body molt, as on this individual photographed 9 June 2007. The coloration of the centers of the throat feathers is variable (white to nearly black), but the throat of most adult females appears uniformly white or only weakly patterned. Adult females with distinctly darker-centered throat feathers are more similar to juvenile males, but most juvenile males have one or more iridescent gorget spots.

Adult females have an indentation on the end of P6 **(B)**; this mark is rounded on juvenile females. However, this character is not visible in many photos. Much more conspicuous are crown and face feathers lacking pale fringes, coupled with more-worn rectrices **(C),** especially R3 and R4. Note that the feathers of the vent **(D)** are worn and not fluffy.

white terminal spot on R3, primary shape (if photos are good enough), and, to a lesser extent, relative bill length. Obviously, without in-hand examination we cannot discount that some age or sex misidentifications occurred, but we believe that these were relatively few and would be unlikely to substantially influence general patterns observed—especially for adults.

We examined photographs to determine sex and age. Then plumage was scored as follows: **Fresh** (bright and colorful with fresh edges); **None** (no sheathed feathers observed); **Holes** (holes or gaps in plumage but no sheathed feathers observed); **Mixed G** (more than one feather generation visible but no sheathed feathers observed); and **Sheathed**. Sheathed feathers were counted and further categorized as follows: 1, 2–4, 5–10, or 10+.

Adult Molt

Hummingbirds have relatively few feathers; for example, the Ruby-throated Hummingbird has only 940 feathers (Wetmore 1936). Their feathers are proportionately large, and missing feathers tend to be more obvious than on other birds. Missing feathers produce an obvious hole or gap in the plumage that is exaggerated by the gray bases of exposed adjacent feathers. Beginning as early as mid-May, some adults show small to large holes in their plumage and, as the summer progresses, most adults appear very worn or obviously tattered. Wear is most obvious on females (Fig. 4), and wear on the underparts of females is often referred to as the "nest mark."

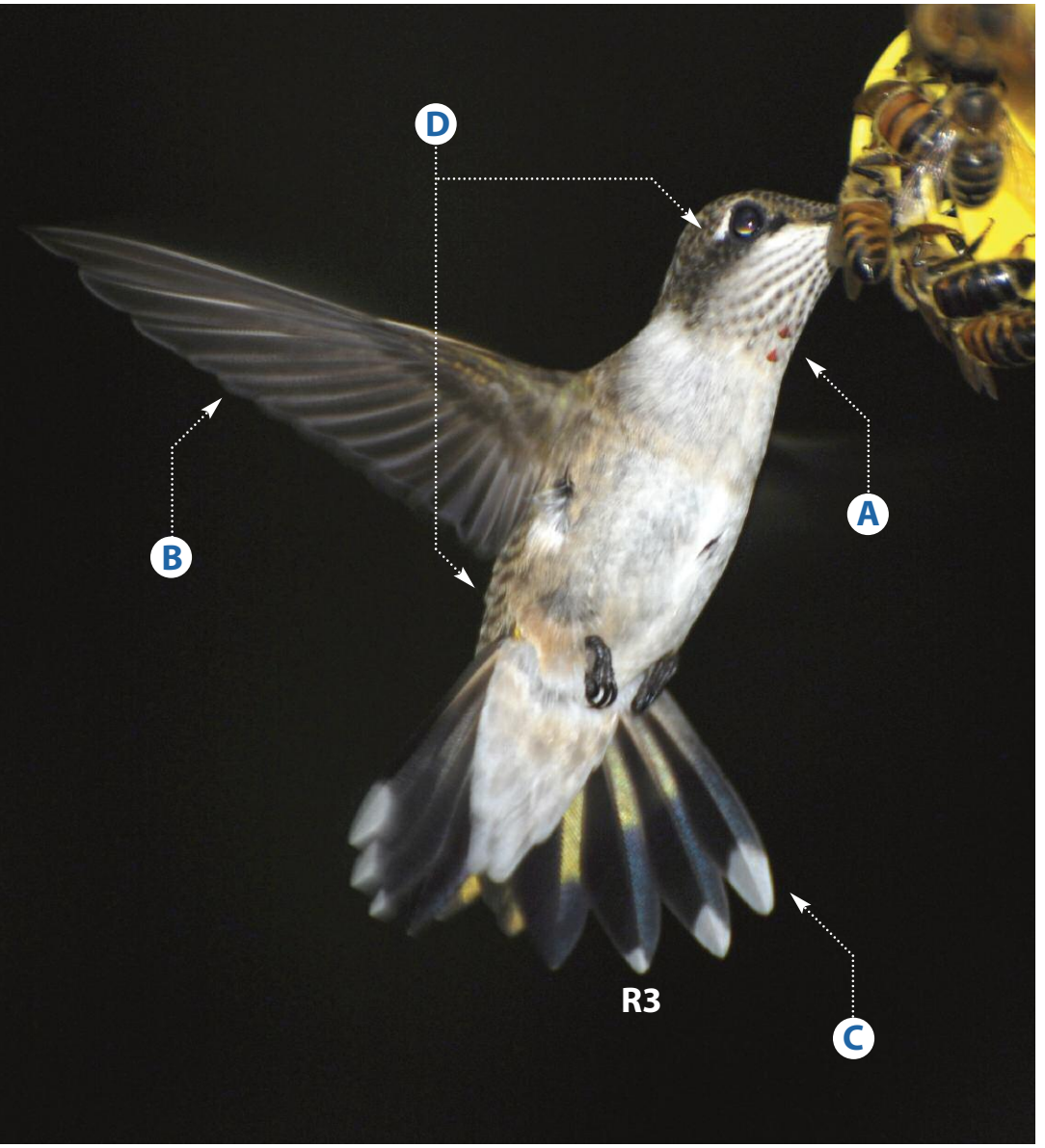

Fig. 7. Immature males usually have one or more iridescent gorget feathers **(A)** and throat feathers, typically with distinct dark centers, as on this individual, photographed 1 August 2007. Note that some immature males can have all-white throat feathers. Immature males have pointed P6s **(B),** which are rounded on immature females, and immature males have less-rounded R5s **(C).**

This individual shows the characteristic scaly head and upperpart feathers **(D)** of juveniles; in this case, only the sides of the rump are visible. The buffy wash on the underparts suggests that these feathers have been recently replaced, whereas other feathers on this bird have a grayish translucence more typical of worn feathers. Bill corrugations shown by juveniles (retained to a lesser degree by some adults, according to Linda Beall) were generally not discernable with the photographic techniques we used and were of little assistance with aging birds in this study.

Immature males have a smaller white spot on R3 than do immature females. Note that R3 is fresh; an adult female would have a worn and blunt-tipped R3 (and R4).

Presence of holes or tattered plumage, however, does not automatically indicate active molt because, unless sheathed feathers can be detected, it's uncertain whether a particular bird is molting or has become more worn and patchy-looking as a result of day-to-day activities. Incoming sheathed feathers also tend to be somewhat more conspicuous on hummingbirds than on other birds, especially on the head and underparts. By the third week of June, most adults show a few to many sheathed feathers (Figs. 9 and 10). By late July and early August, some individuals are in such heavy molt that they initially appear to be diseased or louse-infested (Fig. 11). The progression of molt observed during the summer appears similar to that described for the prebasic body molt on the wintering grounds (Baltosser 1995): Molt of body feathers initiates posteriorly (beginning with the lower rump and back) and generally progresses anteriorly to the head, concluding with the throat.

New body feathers appear identical to those attained during molt on the wintering grounds. Although iridescent feathers are fairly resistant to wear and are difficult to identify as worn without close inspection, there are other clues that individuals have replaced body feathers. In fresh plumage, males have a peach-colored bloom to the pale collar (feathers fade white with time) below the gorget. Females have uniform grayish-white, not worn, underparts (see Fig. 4d), along with a rusty or buffy wash to the sides, flanks, and undertail coverts—although some individuals are brighter than others and retain a buffy

Fig. 8. This **juvenile male** was photographed 26 August 2007. Note that it has very white throat feathers; most juvenile males, however, have dark-centered throat feathers, resulting in a "five-o'clock shadow" look. This individual also has new green feathers on the sides of the breast **(A)** and possibly also on the crown **(B),** indicating two generations of feathers. Except for a possible sheathed feather on the breast, this bird shows no obvious active molt. Note the "bulge" around the neck and the portly appearance overall, suggesting heavy subcutaneous fat and imminent departure on southbound migration.

wash even when relatively worn. When fresh and unworn, both sexes exhibit puffy white femoral tufts, most noticeable behind the legs when hovering.

Adults sometimes show a patchwork of new and old or disheveled feathers on the back by early June. Unfortunately, this patchwork pattern is not well documented by our method of photography (as compared to molt on the head and underparts) unless it is extensive (Fig. 12). An interesting aspect of the summer molt is that gorget replacement in adult males is gradual and overlaps with the rest of body molt (Fig. 13), as opposed to being the "grand finale" of the molt, as on the wintering grounds. An example is the phenomenon of "rapid regorgetation," in which males dramatically conclude their winter molt by replacing their entire gorget in a matter of a few days, as described for the Calliope Hummingbird by Dittmann and Demcheck (2006).

On the wintering grounds, prebasic molt reportedly spans five-plus months (Pyle et al. 1997), and we detected summer-molting Ruby-throats over a period nearly as long (Figs. 9 and 10). For an individual bird, however, this molt is probably compressed into a much shorter period, perhaps as short as one month. For example, a worn female on 28 July was fresh on 1 September (Fig. 4). This conclusion is reinforced by our observations of males with sheathed gorget feathers only from mid-July through late August, and by the extent of sheathed feathers observed on many adults of both sexes at the apparent peak of their summer molt. Unfortunately, during this preliminary work we did

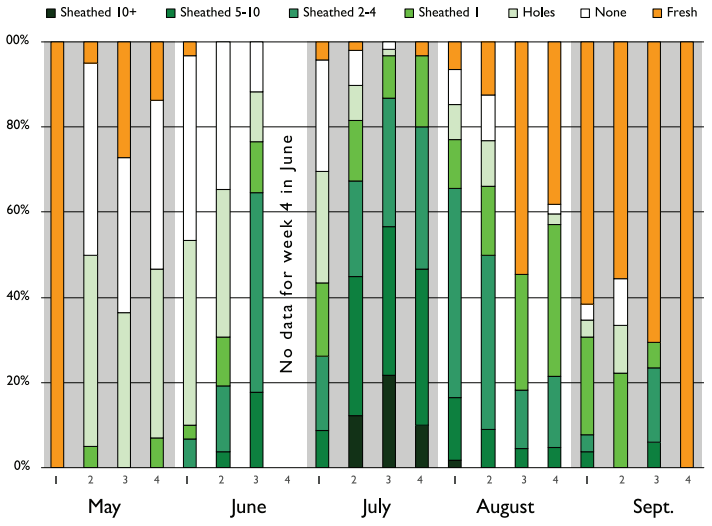

Fig. 9. This chart shows the relative percentage of molt activity of **adult male** Ruby-throated Hummingbirds photographed during 2006 and 2007; birds showing two generations of feathers, but no active molt, are included in the "None" category. No photographs were obtained during the fourth week of June. Tantalizing is the suggestion of two peaks of molt for males. It is possible that the first peak involves males that initiated molt subsequent to successful copulations related to second broods, whereas the second peak involves "unsuccessful" males that extended their courtship period and delayed molt. Alternatively, the second peak could reflect a "molt-migration stopover" of migrant males; this phenomenon, however, has not been reported at hummingbird banding and monitoring stations where only migrants occur. *Graph © by Kei Sochi.*

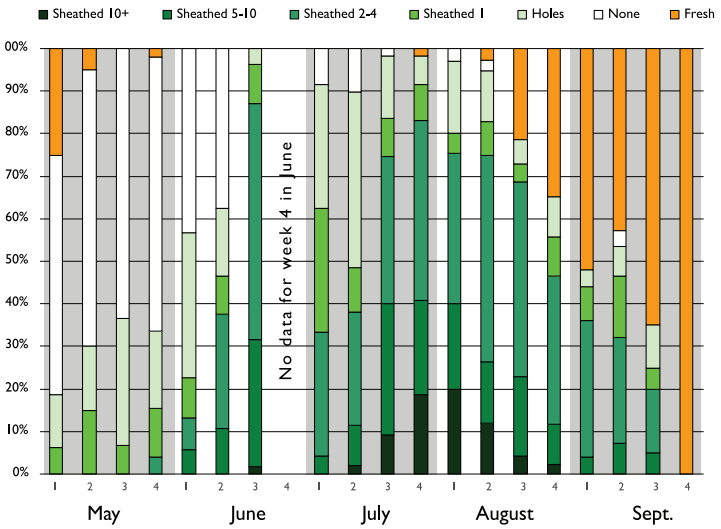

Fig. 10. This chart shows the relative percentage of molt activity of **adult female** hummingbirds photographed during 2006 and 2007; birds showing two generations of feathers, but no active molt, are included in the "None" category. No photographs were obtained during the fourth week of June. As with adult males (Fig. 9), the data may suggest two molt peaks. If confirmed, one possible explanation for this bimodal pattern would be that "single-brood" females molt earlier than "double-brood" females. *Graph © by Kei Sochi.*

not have any marked birds for properly documenting progression of molt for particular individuals; we hope we will be able to address this deficiency in the near future by observation and recapture of marked and banded individuals.

The high percentage of individuals with active, extensive body molt is documented in Figs. 9 and 10. There is also a strong summer temporal pattern (Figs. 9 and 10). These results argue against adventitious feather replacement—that is, the replacement of feathers accidentally lost. Thus, we believe that, in addition to the molt which occurs on the wintering grounds, Ruby-throated Hummingbirds undergo an extensive replacement of body feathers on the breeding grounds. Because Ruby-throated Hummingbirds are thought to undergo a single complete molt on the wintering grounds, an alternative hypothesis might be that observations of summer molt pertain to individuals getting a "head start" just before or during the southward migration. This would imply that the annual molt is more protracted than previously believed.

However, this "head start" hypothesis seems unlikely because our data suggest a more-or-less complete summer replacement of body plumage in most adults. If winter molt typically concludes in February and March just prior to spring migration, then we would expect to see many birds arriving in spring with very worn feathers, especially in the ventral plumage of adult females, because so many of the body feathers had been replaced six to seven months in advance of spring migration. Also, if the summer molt we have documented were the beginning of a protracted winter molt, then we would continue either to see birds with active molt or to note partially molted plumage throughout the fall. But we have observed neither. Because a high percentage of adults observed after mid-August appear fresh and unworn—most notably adult females that lack "nest marks"—we are confident that the summer molt is a separate phenome-

Fig. 11. This photo is typical of those obtained for this study. Note that because only a portion (ventral or side view) of the plumage can be examined, such an image represents a minimum estimate of actual molt. This **adult female,** photographed 12 August 2006, has nearly the entire throat in pinfeathers; the throat has more than 10+ sheathed feathers, and this individual would be scored as 10+. The underparts are obviously missing many feathers, resulting in a tattered or unkempt look, with only a few sheathed feathers visible. Note the blunt-tipped R4 and pointed R5, which support identification as an adult female.

non, and that Baltosser (1995) was incorrect in stating that all adult Ruby-throated Hummingbirds migrate south in worn body plumage.

Because a *complete* late winter-early spring molt is documented by specimen evidence (Baltosser 1995, Pyle et al. 1997), we conclude that replacement of body feathers during the summer represents replacement of at least some body feathers for a second time, which, by definition (Humphrey and Parkes 1959), qualifies as a distinct molt. Summer molt has been documented elsewhere, for example both in Virginia <pbase.com/shellyva/ruby_throated_hummers> and in Pennsylvania <westol.com/%7Ebanding/Pictorial_Highlights_August_2003.html>, making it unlikely that our local population of Ruby-throats exhibits an anomalous molt schedule.

Juvenile Molt

We photographically documented summer body molt on juveniles of both sexes, including evidence of sheathed body feathers from late May through September (Figs. 14 and 15). But summer body molt in juveniles is not as dramatic or conspicuous as in adults (Fig. 16). Without repeated in-hand examinations of marked individuals, the extent of summer feather replacement in these young birds remains unclear. We have observed a few juveniles with many sheathed, non-gorget, feathers, whereas others (both males and females) can appear fresh until late September. Substantial numbers of juveniles possessed two generations of feathers, especially males (Fig. 17), and we detected individuals with one or a few sheathed feathers on the throat.

We suspect (but have not verified) that

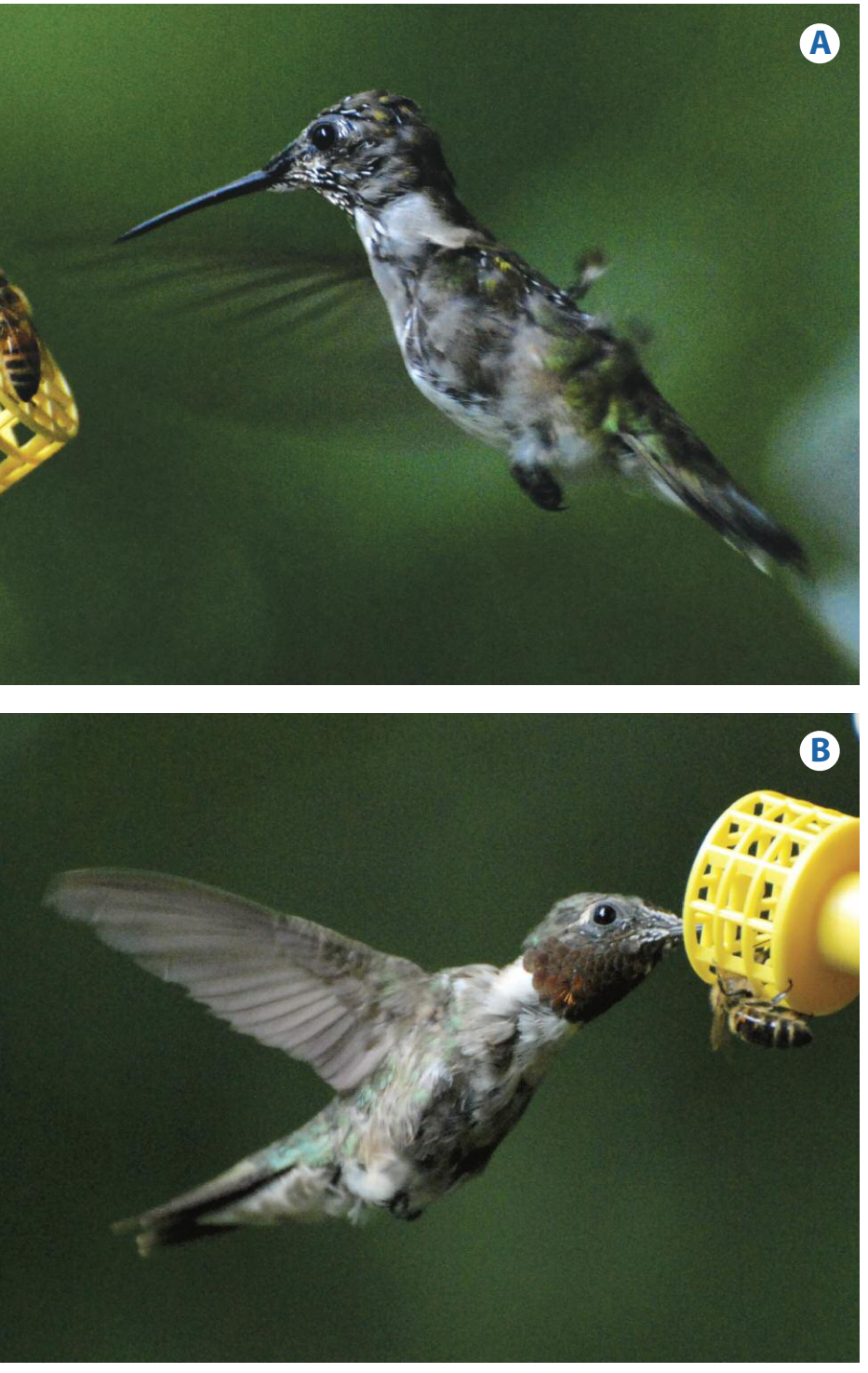

Fig. 12. These two adults were photographed during July. The **adult female (A),** photographed 30 July 2007, shows extensive molt with sheathed feathers clearly visible on the back and head, illustrating the potentially rapid progress of the summer molt. The **adult male (B),** photographed 17 July 2007, has most of his face covered with incoming sheathed feathers. The rumpled appearance of the underparts may suggest missing feathers.

early autumn is when immature males acquire their first red gorget feathers. Hummingbird bander R. R. Sargent (personal communication) reports that he has never observed iridescent gorget feathers on the many nestlings he has examined, further supporting the hypothesis that these feathers are not part of the juvenile plumage. We also noticed acquisition of other adult-type feathers such as iridescent green feathers on the sides. Otherwise, it is unclear whether a second set of feathers is involved in other regions of the plumage—for example, mixed patches of "dull" vs. "bright" iridescent green feathers on the upperparts, especially the crown (Fig. 8). Many juveniles also showed small holes in the plumage suggesting molt, but, as mentioned earlier, this trait cannot be used as evidence to document molt because such areas of missing feathers could result from accidental loss through intraspecific aggression, attacks by predators, etc.

Flight Feathers

We photographed a few individuals, including both adults (Fig. 18) and juveniles, with missing or growing primaries and rectrices. Although one adult female had the first primary (P1) sheathed, which is suggestive of the onset of prebasic molt, another four birds had other primaries sheathed or missing, perhaps better suggesting adventitious replacement or loss. No juveniles were photographed with missing or molting primaries. A few adults (n=6) and juveniles (n=5) were photographed with molting or missing rectrices.

Because these individuals did not also show signs of active primary molt, we concluded that their rectrices had most likely been lost accidentally; hummingbirds can lose rectrices in a variety of ways. For example, on 24 September 2006, the first author observed a male Summer Tanager attempt to capture a juvenile Ruby-throat in flight; this close encounter resulted in the escape of the hummingbird but at the expense of losing some or possibly all of its rectrices. It is not unusual to see the occa-

Fig. 13. This **adult male,** photographed 30 July 2007, shows active body molt. Note the several sheathed gorget feathers. Incoming sheathed feathers on the breast are not as conspicuous as plumage "holes" resulting from missing feathers. During the molt on the wintering grounds, the gorget is generally replaced last, but that does not seem to be the case with the summer molt. Note the buffy cast of fresh feathers on the throat and underparts.

sional hummingbird missing feathers or even the entire tail.

The Alternate Plumage of the Ruby-throated Hummingbird

Our observations and those of others appear to provide adequate evidence, at least for adults, that Ruby-throated Hummingbirds replace body feathers twice in an annual molt cycle. If this is the case, then the names of these molts and their corresponding plumages need revision, and several approaches could be taken to accomplish this. Following the traditional Humphrey-Parkes ("H-P") system of molt classification and terminology (Humphrey and Parkes 1959), the complete molt of adult Ruby-throats on the wintering grounds would continue to represent the definitive prebasic molt (producing definitive basic plumage) and the primary reference point (for wing and tail molt) of the species' molt cycle. But what are the true parameters of the prebasic molt in view of the "summer molt"?

Focusing on adults first, the logical questions include the following. First, should the summer molt be considered completely disconnected from the molt on the wintering grounds? Or, second, should the newly described summer body molt be treated as the beginning of the traditional prebasic molt, involving feather replacement following breeding? And, third, if so, then do we need to reevaluate the well-documented late winter–early spring body molt on the wintering grounds?

If we choose the first option, then the summer molt would represent a second (or "alternate") molt of the body feathers and be categorized as the *definitive prealternate molt*, with the resultant new body plumage known as *definitive alternate plumage*. This

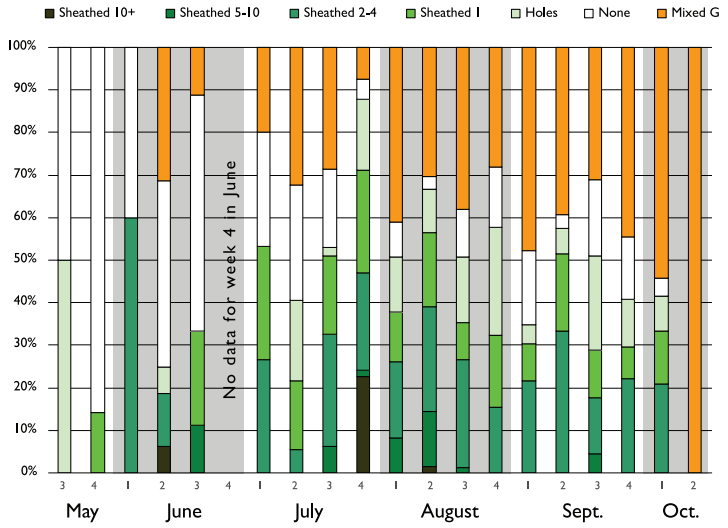

Fig. 14. Immature males. *Graph © by Kei Sochi.*

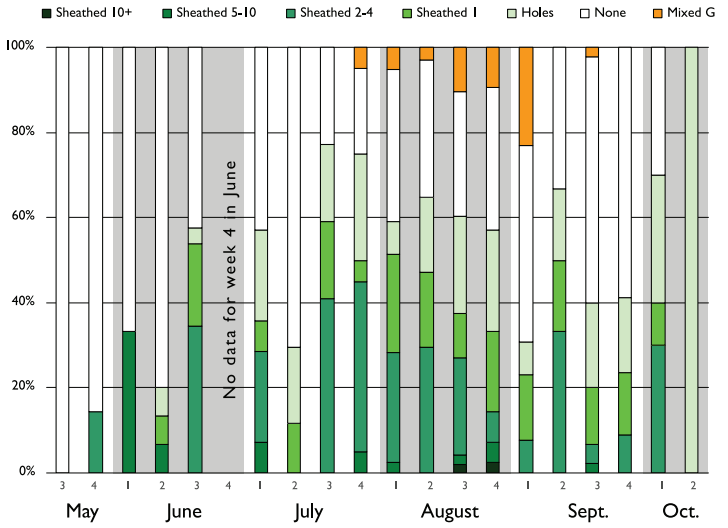

Fig. 15. Immature females. *Graph © by Kei Sochi.*

These charts show the relative percentage of molt activity on juveniles photographed during 2006 and 2007. The most conspicuous second-generation feathers are male iridescent gorget feathers, and probably for that reason, many fewer females were detected with second-generation feathers. Especially interesting is the high percentage of immature males showing multiple generations of feathers ("mixed G") but no active molt. This result may suggest that molt in immatures is more gradual and less extensive—and generally much less conspicuous—than molt in adults. Because a brood can be produced every 36–48 days (Robinson et al. 1996), at least two broods are probably raised each year at our study site.

molt and plumage are not previously described for hummingbirds. Now, in matters of molt, as often as not, things are more complicated than they at first appear, and we prefer the second and third scenarios in the preceding paragraph. They make more intuitive sense. Under this interpretation, the summer molt would be designated as the definitive prebasic body molt; the "winter" body molt, then, would become the definitive prealternate body molt that coincidentally overlaps with the conclusion of the prebasic wing and tail molt. This overlap has probably obscured the distinctness of the prealternate molt.

Regarding juveniles, the percentage of body feathers that is replaced prior to or during fall migration needs further investigation. Pyle et al. (1997) speculated that acquisition of iridescent gorget feathers by immature males in late summer and fall represents a "supplemental molt" rather than early onset of the prebasic molt. The percentage of red gorget feathers we observed on immature males ranged from zero to nearly 50% of the gorget, but, typically, iridescent gorget feathers were few, scattered, or in small clusters. Although our sample size of wintering immature male Ruby-throated Hummingbirds is small, it supports the existence of a "supplemental molt" because individuals that arrive in early winter (November–December) with some iridescent gorget feathers generally retain the same throat pattern all winter. These individuals then replace the entire gorget between March and mid-April.

This rapid partial body molt in the early spring was previously considered the finale of the prolonged prebasic molt. When viewed in the context of our revised adult molt cycle, however, it makes more sense that this phenomenon in immatures pertains to a first prealternate molt. This would mean that yearlings arrive on the breeding grounds in spring in first-alternate plumage.

Clearly, the naming of evolutionarily modified molts and their resulting plumages is fraught with complexity and beyond the scope of this article. Because the H-P system provides a solid foundation for the nomenclature of post-juvenile molts and plumages, we prefer its "traditional" usage. The H-P system is useful because it provides a functional system that does not rely on descriptive terms dependent on temporal, seasonal, and reproductive conditions to name plumages and molts. Although the H-P system is not universally accepted, neither is the "modified H-P system" of Howell et al. (2003),

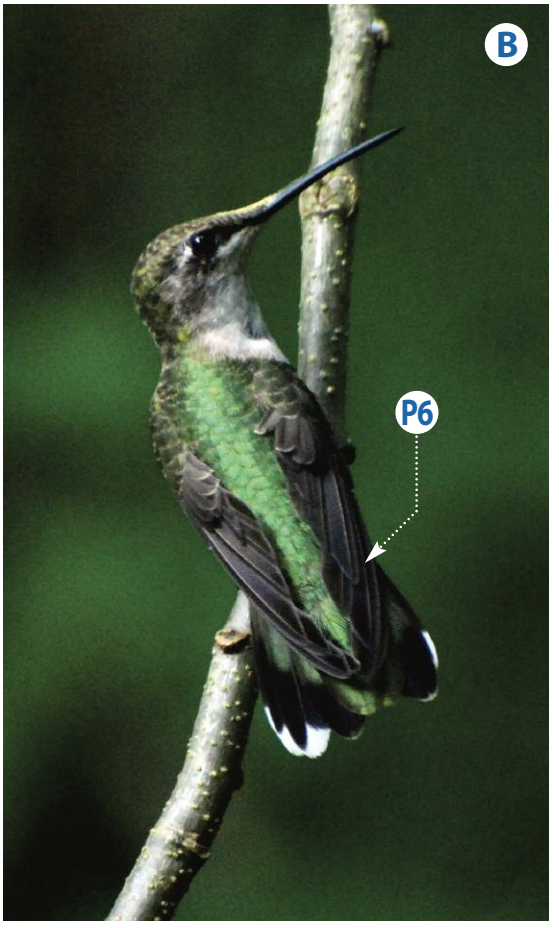

Fig. 16. Compare the **juvenile** from a first brood photographed 28 May 2007 **(A)** with the **juvenile** photographed 18 July 2007 **(B).** Both individuals are readily identified as juveniles by the pale-edged feathers of the crown, creating a scaly appearance. Note that the upperparts of the juvenile photographed later in the summer **(B)** show some wear on the pale edges of the crown and tail feathers.

Juvenile females have more-pronounced pale edges to the inner secondaries ("tertials") and retain these longer than do juvenile males. In the case of the individuals shown here, sex can only be guessed based on that character. The tip of P6 (rounded in juvenile females vs. pointed in juvenile males) suggests a female, but we cannot be certain. Neither individual shows any sign of active molt.

which was introduced to readers of *Birding* in a two-part series on "All You Ever Wanted to Know About Molt" (Howell 2003a, 2003b). This modification redefines juvenile plumage as the "first basic plumage" and *inserts within what previously would have been considered the juvenile cycle* one or more non-definitive post-juvenile plumages.

For the sake of thoroughness, we address how Howell et al. (2003) would assess molt in yearling Ruby-throated Hummingbirds. In their system, the *first complete molt on the wintering grounds* is the preformative molt; thus, second-calendar-year Ruby-throats return in spring in *formative plumage*, which looks identical to definitive plumage, at least in the case of Ruby-throated Hummingbirds. The summer molt of juveniles (for example, gorget feathers of males) would represent an additional preformative molt, termed "PF1a" (preformative 1a) or auxiliary preformative molt by Pyle (2008). An alternative suggestion by P. Pyle (personal communication) is to consider the summer molt of juveniles as the preformative molt and the first complete overwinter molt as the second prebasic molt.

Final Thoughts

The summer molt of adult Ruby-throated Hummingbirds has been largely overlooked due to a combination of factors. An important point is that molt primarily occurs on the breeding grounds in breeding habitat or nearby staging areas. Thus, molting birds may be infrequent at locations that might host an abundance of migrants but that do not have a local breeding population. Numerous hummingbird enthusiasts live in the city of Baton Rouge within 10–15 miles of our house, but Ruby-throated Hummingbirds are generally absent from feeders there from late May through

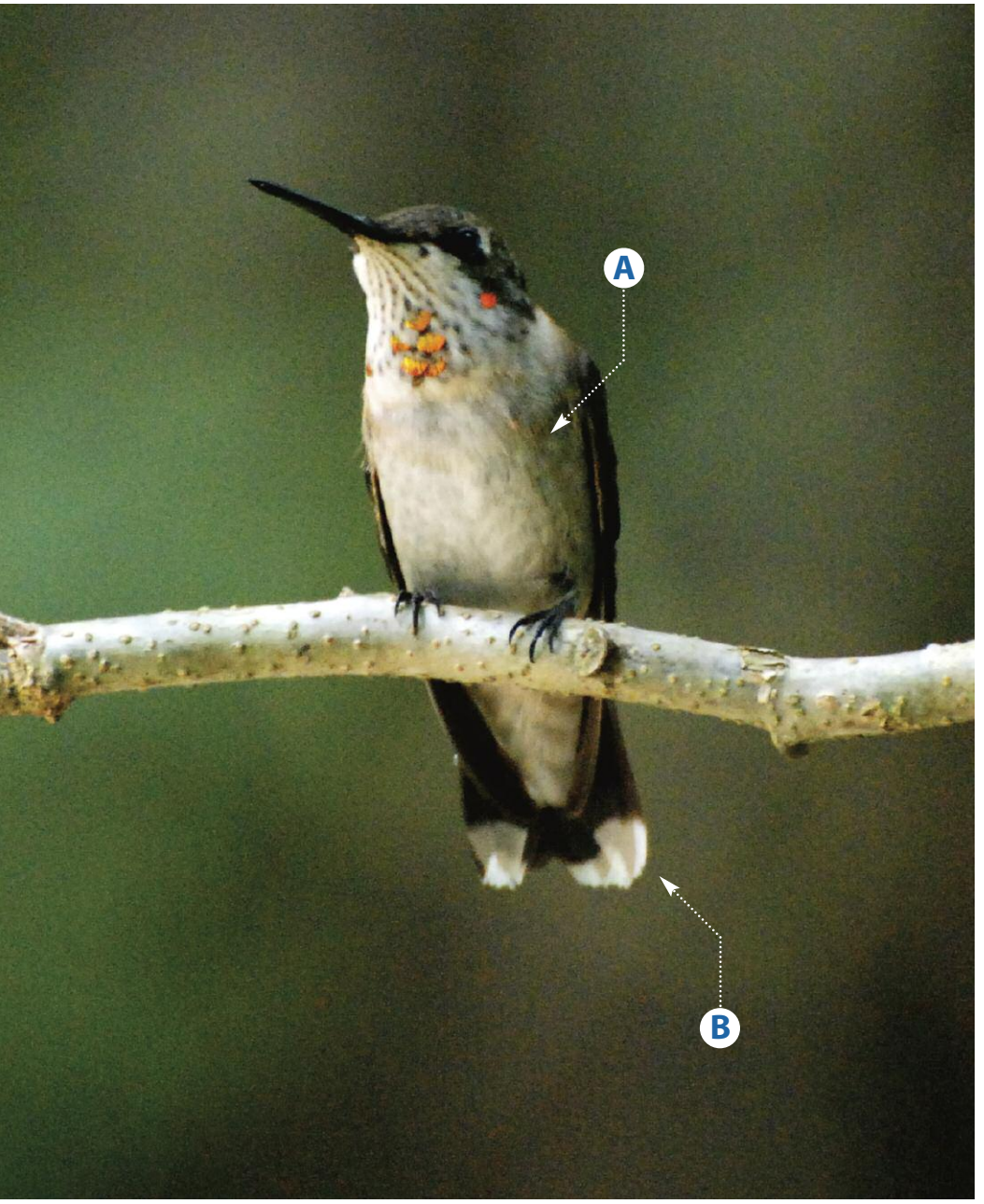

Fig. 17. This **juvenile male** was photographed 19 August 2007. There are eight iridescent gorget feathers, but no sheathed feathers are visible on the throat. Only one incoming sheathed feather **(A)** is visible (on the breast). However, the buffy coloration on the breast suggests other new feathers. The tail tips **(B)** are somewhat ragged, indicating wear.

early July. It's also possible that observers—ourselves included, until we finally paid more attention—just take their summering Ruby-throated Hummingbirds for granted and just don't study them very closely.

Other factors are worthy of consideration. First, summer molt is rapid in nature. Second, body molt of hummingbirds can be difficult to detect on museum specimens, plus there are relatively few specimens taken during this period. Third, body feather wear (especially of iridescent feathers) is difficult to detect in the field (and in hand). Fourth, perhaps observers have been biased by the published literature to assume that there is no molt outside of the "traditional" winter prebasic molt period, and have brushed aside signs of summer molt as adventitious (because hummingbirds are aggressive and combative, and accidental damage or loss of feathers is fairly frequent).

Gaps remain in our knowledge of North American birds, and this study provides yet another example of how birders can make important contributions right from their own backyards. Molt is generally understudied, especially for hummingbirds, and our casual observations of other hummingbird species (for example, Black-chinned and Rufous) suggest that they, too, probably have a summer body molt. Observers in areas with other breeding species should be on the lookout to better document the summer molt phenomenon.

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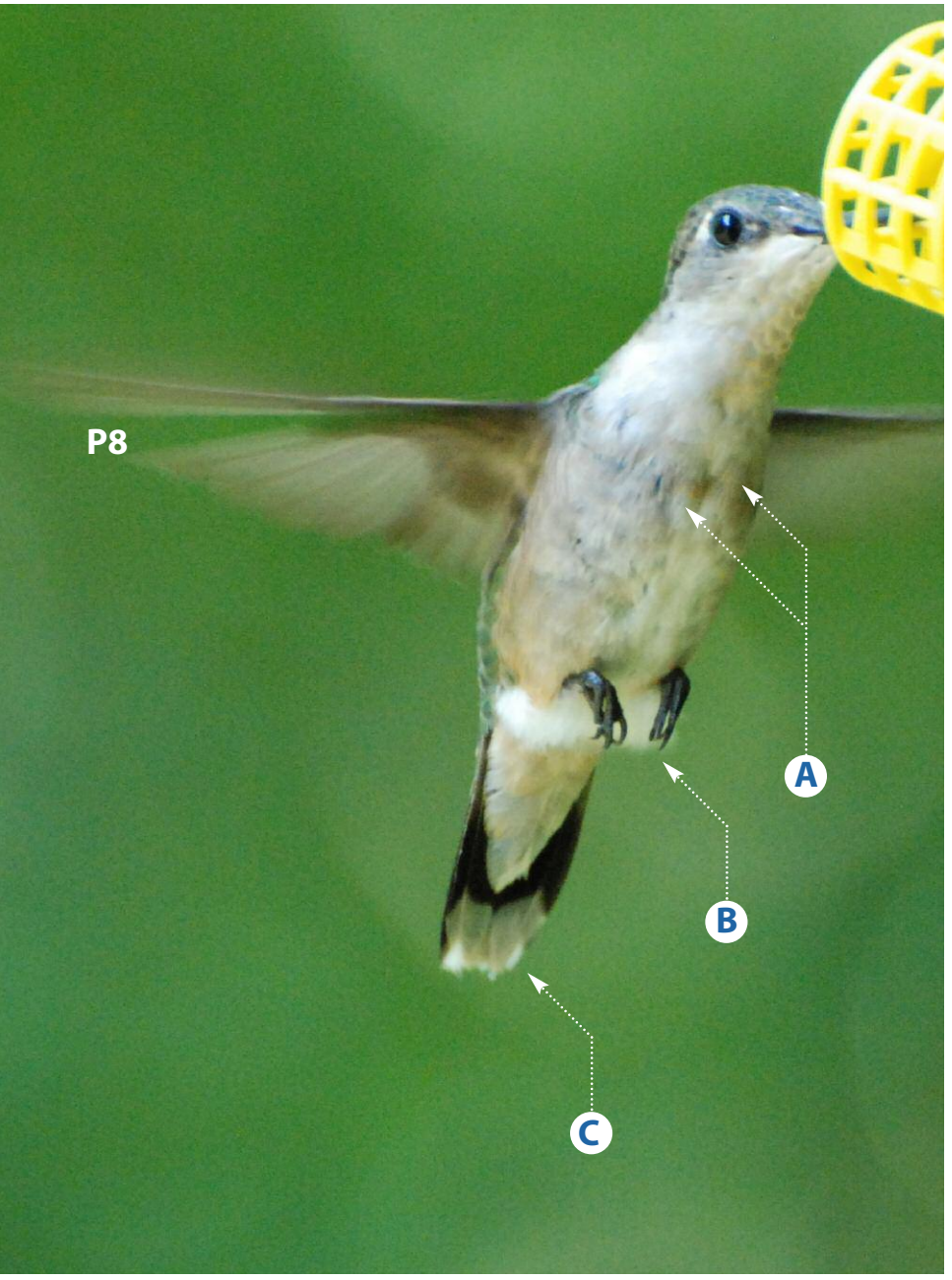

Fig. 18. This **adult female** photographed 24 August 2007 is missing a primary, probably P8; P1 may also be missing. This bird is in the process of replacing abraded underpart feathers (creating the "nest mark"), and a couple of sheathed (incoming) feathers are visible **(A).** The femoral tufts behind the legs are fresh and fluffy **(B),** but the rectrices **(C)** are worn, tattered, and blunt-tipped. Both adults and juveniles were photographed with missing or sheathed primaries or rectrices. One case, involving an adult female with P1 growing in, suggests the beginning of primary molt, but other cases, such as this one, clearly represent adventitious molt.

V. Remsen for access to the bird collection.

Literature Cited

Baltosser, W.H. 1995. Annual molt in Ruby-throated and Black-chinned Hummingbirds. *Condor* 97:484–491.

Dittmann, D.L., and D.K. Demcheck. 2006. Contributions to our knowledge of molt in Calliope Hummingbird. *Birding* 38(6):32–40.

Howell, S.N.G., C. Corben, P. Pyle, and D.L. Rogers. 2003. The first basic problem: A review of molt and plumage homologies. *Condor* 105:635–653.

Howell, S.N.G. 2003a. Understanding molt: Part I. The variety of molt strategies. *Birding* 35:490–496.

Howell, S.N.G. 2003b. Understanding molt: Part II. Finding order amid the chaos. *Birding* 35:640–650.

Humphrey, P.S., and K.C. Parkes. 1959. An approach to the study of molts and plumages. *Auk* 76:1–31.

Lopez-Calleja, M.V., F. Bozinovic, and C. Martinez del Rio. 1997. Effects of sugar concentration on hummingbird feeding and energy use. *Comparative Biochemistry and Physiology* 118a:1291–1299.

McWhorter, T.J., and C. Martinez del Rio. 2000. Does gut function limit hummingbird food intake? *Physiological and Biochemical Zoology* 73:313–324.

Pyle, P., S.N.G. Howell, and G.M. Yanega. 1997. Molt, retained flight feathers, and age in North American hummingbirds, pp. 155–166 in: R.W. Dickerman, ed. *The Era of Allan R. Phillips: A Festschrift.* R.W. Dickerman, Albuquerque.

Pyle, P. 2008. *Identification Guide to North American Birds. Part II. Anatidae to Alcidae*. Slate Creek Press. Point Reyes, California.

Robinson, T.R., R.R. Sargent, and M.B. Sargent. 1996. Ruby-throated Hummingbird (*Archilochus colubris*), in: A. Poole and F. Gill, eds. *The Birds of North America*, no. 204. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington.

Wetmore, A. 1936. The number of contour feathers in passeriform and related birds. *Auk* 53:159–169.

Glossary of Terms

Definitive Plumage. In Humphrey-Parkes terminology, a plumage that *does not change further with age*. This is functionally equivalent to "adult" plumage.

Basic Plumage. The plumage "basic" to each species of bird, thought to be the "original" or "ancestral" plumage. Typically, it is the plumage that follows a complete molt sometime after breeding. Although functionally equivalent in many bird species to non-breeding or winter plumage, basic plumage is *not defined with regard to timing or breeding condition*, except that for most birds timing of replacement is more or less on an annual cycle.

Alternate plumage. Merely *another plumage inserted into the annual cycle*. It is often, *but not always*, equivalent to breeding or "nuptial" plumage. (All birds have a basic plumage; some also have an alternate plumage.)

Juvenile plumage. The first covering of true, pennaceous (structurally adult-like) feathers, which can usually be distinguished from adult feathers by the softer, looser-textured character of body feathers and by a different shape of the flight feathers (typically narrower and more tapered on juveniles). For commentary on "juvenal" vs. "juvenile" plumage, see pp. 14–15 in this issue of *Birding*.

How Many Hummingbirds?

It is difficult to be certain about how many hummingbirds visit a particular yard on any given day. One method is to extrapolate from "maximum-in-view-at-once" counts (at feeder arrays). Observations from banding stations suggest that the total number of individuals frequenting an array may be as much as ten times higher. A summer count of 20–30 in view at a time would therefore potentially translate into feeder attendance by 200–300 individuals. Louisiana banders Nancy L. Newfield and Linda Beall suggest a more conservative estimate of five times the number of birds in view at a time, which would lower our population estimate to 100–150. Regardless, there is likely to be considerable variation in the total number of birds from site to site.

Rate of sugar consumption also has been suggested as a means of estimating numbers. When we have honey bee-free summer months, we assume most sugar solution is consumed by hummingbirds. Our summer consumption averages about one gallon of solution per day, which is equivalent to approximately 1,262 grams of sugar per day. We estimate that a breeding Ruby-throated Hummingbird requires two grams of sugar per day. This estimate is based on studies of the closely related Black-chinned Hummingbird, which has a mass of 3.6 grams (about the same as a Ruby-throat) and requires 1.76 grams of sugar daily. After a few adjustments for sugar consumption based on solution concentration (Lopez-Calleja et al. 1997, McWhorter and Martinez del Rio 2000), we arrive at a figure of 631 hummingbirds per day.

On four days between late April and mid-July 2008, Linda Beall, with assistants Linda Keefer and Linda Juneau, banded and marked (with forehead paint) more than 267 Ruby-throats around our feeding operation. These were presumed local breeders, as nearly all females were in breeding condition, and males had little or no fat. Observations in the days immediately following the last banding/marking session revealed substantial numbers of unmarked adults, sometimes two or three at a time. In our yard, at least, the 10×-in-view-at-once rule of thumb may be a reasonable predictor of actual hummingbird numbers.