

THE TIMING AND RELIABILITY OF BILL CORRUGATIONS FOR AGEING HUMMINGBIRDS

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The extent of corrugation on the bill has proven a useful method in determining the age of hummingbirds (Ortiz-Crespo 1972, Stiles 1972, Baltosser 1987, Russell 1996). Nestlings and postfledging juveniles have soft bills with deep corrugation, covering 50% or more of the bill, whereas adults have harder bills with little or no corrugation. Presumably, the corrugation is lost by a combination of the bill-hardening process and wear, but little has been published on the mechanics or timing of corrugation loss. If hummingbirds retain at least some corrugation at the base of the bill beyond the first prebasic molt (at which point juveniles assume adult plumage; Bent 1940, Stiles 1972, Baltosser 1987), our ability to age them through or beyond the first annual cycle could be enhanced.

To investigate the rate of bill smoothing, we selected the Anna's Hummingbird (*Calypte anna*) because of its year-round abundance in California, being well represented both in museum collections and in the banding records of the Point Reyes Bird Observatory (PRBO). The extremely protracted breeding season of this species, late December through spring and sporadically through summer (Bent 1940, Yanega unpubl. data), results in wide variation in the age of individuals (thus, extent of bill smoothing) on a given date, obscuring precise estimates of smoothing rates in individual birds. Therefore, we also examined bill corrugation in the Rufous Hummingbird (*Selasphorus rufus*), which has a shorter breeding season, late April to mid-July (Calder 1993).

METHODS

Our analysis is based on 496 Anna's Hummingbirds (146 museum specimens, 350 banding records) and 218 Rufous Hummingbirds (131 museum specimens, 87 banding records). Specimens of all Anna's and most Rufous Hummingbirds were from the collections at the California Academy of Sciences (CAS), Moore Laboratory of Zoology (MLZ), Museum of Vertebrate Zoology (MVZ), and PRBO. To augment our sample of fall and winter Rufous Hummingbirds (collected in Mexico), we also examined specimens at the Natural History Museum of Los Angeles County (LACM), San Diego Natural History Museum (SDNHM), and Western Foundation of Vertebrate Zoology (WFVZ). Specimens of Anna's Hummingbirds were taken from throughout the species' breeding range, although a majority were collected in the San Francisco Bay area. Banding records were compiled from 1980 to 1993 at PRBO's Palomarin field station north of San Francisco (DeSante and Geupel 1987).

On each bird, the proportion of the ramphotheca (lateral surfaces of the bill) that contained corrugation (Ortiz-Crespo 1972, Baltosser 1987) was

BILL CORRUGATIONS FOR AGEING HUMMINGBIRDS

estimated to the nearest 5% (see Figure 1). Scoring of banded birds was performed by numerous banders at PRBO. Scoring of specimens was performed by Yanega (all Anna's and most Rufous Hummingbirds) and Pyle (42 specimens of the Rufous Hummingbird). Prior to Pyle's scoring, data collection was standardized by comparing scores of both observers on > 50 specimens at CAS, until estimates by each observer differed by no more than 10%.

We independently aged and sexed each specimen by plumage and flight-feather shapes (Williamson 1956, Stiles 1972, Baltosser 1987, Russell 1996, Pyle et al. in press). Juveniles can be separated from adults through at least the prebasic molt, which occurs from May to October in Anna's Hummingbird and from September to January in the Rufous Hummingbird (Pyle et al. in press); some male Anna's Hummingbirds also can be aged through their second prebasic molt by incomplete gorgets or retained flight feathers (Russell 1996, Pyle et al. in press).

Smoothing rates were calculated by means of linear regressions. We incorporated date as the dependent rather than the independent variable to predict the mean smoothing duration of an individual rather than that of the entire population (Pimm 1976). Quadratic date terms (date^2) were incorporated into regressions to assess the linearity of the relationship between corrugation loss and time. Regression equations combined with "forecasted" standard deviations (Computing Resources Center 1992) were used to

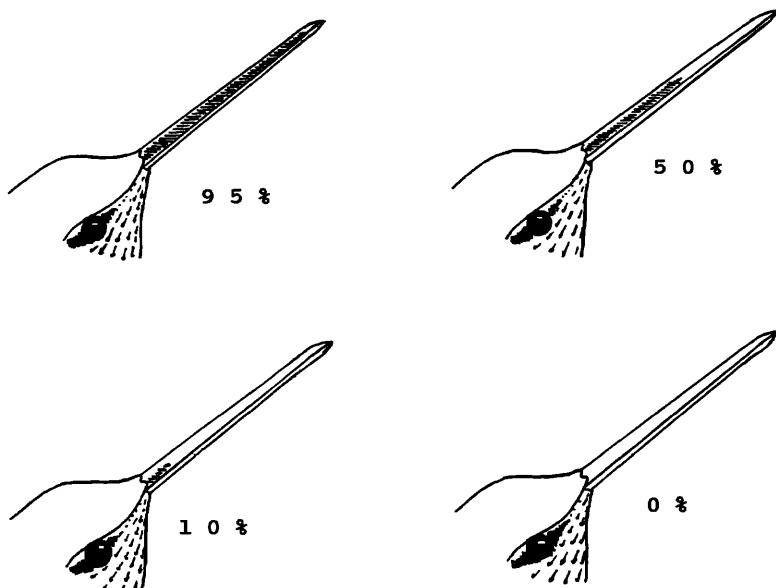


Figure 1. Hummingbird bills with different proportions of corrugation.

BILL CORRUGATIONS FOR AGEING HUMMINGBIRDS

predict 95% confidence intervals for dates in which first-year birds complete the smoothing process.

RESULTS

Retention of Bill Corrugation in Adults

Previous studies have assumed that adult hummingbirds lose bill corrugation entirely, or at most retain only superficial notching at the base of the bill. Our data show that Anna's Hummingbirds beyond 12–15 months of age can retain corrugation on up to 10% of the bill. Of 23 banded birds recaptured at Palomarin and known to be >14 months old, 14 had 0% corrugation, six had 5% corrugation, and three had 10% corrugation. One bird (band 24569), a female captured as a juvenile on 6 June 1981, still retained 10% corrugation when it was recaptured on 28 March 1984, at age 33–39 months. In another sample of banding records, of 45 birds (mostly males) in adult plumage between 15 July and 15 October (thus being >12 months old), 23 had 0% corrugation, 13 had 5% corrugation, eight had 10% corrugation, and one was recorded with 15% corrugation. In a similar sample of 36 museum specimens, 28 had 0%, six had 5%, and two had 10% corrugation. A plot of all banding and specimen data points (Figure 2), furthermore, indicates that Anna's can have 5–10% corrugation at any time of year. Finally, of 18 adult-plumaged male Rufous Hummingbirds collected from August to February (thus at least 12 to 18 months old), 15 had 0%

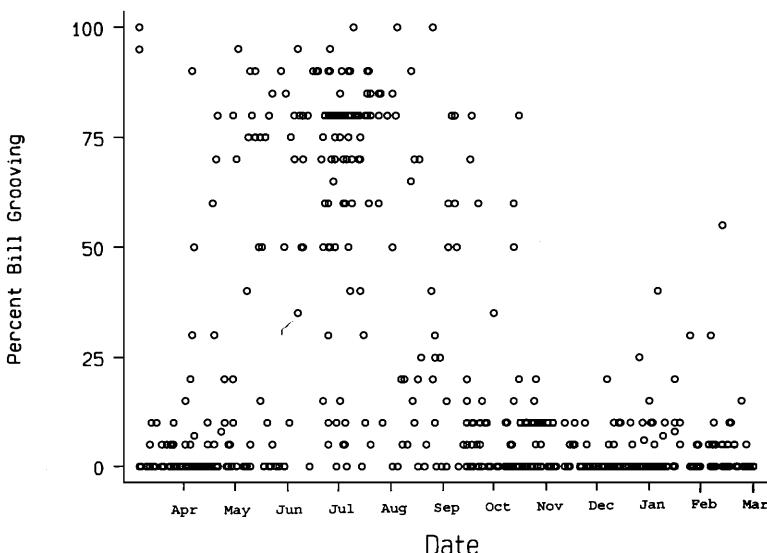


Figure 2. Corrugation proportions by month in Anna's Hummingbirds.

BILL CORRUGATIONS FOR AGEING HUMMINGBIRDS

corrugation, two had 5% corrugation, and one had 10% corrugation. We conclude that adults of both species can retain up to 10% corrugation, with <5% of adult birds retaining a higher percentage. Thus 10% serves as a threshold, above which first-year birds can be separated from adults with over 95% confidence.

Bill Smoothing in Young Birds

We estimated the rate of bill smoothing from regression analyses using birds independently aged as juvenile or second-year by plumage (Figure 3). On the basis of the entire data set, linear terms for both species were highly significant ($t = -6.09, P < 0.001, n = 194$ for Anna's Hummingbird; $t = -12.613, P < 0.001, n = 91$ for the Rufous Hummingbird), whereas quadratic terms for both species were insignificant ($t = -1.18, P = 0.239$ for Anna's; $t = 1.15, P = 0.250$ for the Rufous), indicating a linear relationship between corrugation loss and time. Similar levels of significance were found for all comparisons using specimens only.

The predicted mean date for first-year birds to reach 10% corrugation was 3 November \pm 22 days for Anna's Hummingbird and 25 February \pm 13 days for the Rufous Hummingbird. Thus, on the basis of all data, 95% (estimated as mean \pm twice the standard deviation) of Anna's Hummingbirds reach 10% corrugation between 20 September and 17 December and 95% of Rufous Hummingbirds reach 10% corrugation between 31 January and 23 March. When just the specimen data were used, these predicted dates were 26 October \pm 17 days (95% range 22 September–29 November) for Anna's and 23 February \pm 12 days (95% range 31 January–19 March) for the Rufous.

We inferred hatching dates on the basis of egg and nest data from Bent (1940), Pitelka (1951), Calder (1993), Russell (1996), and Yanega (unpubl. data) and by assuming an average incubation period of 14 days (Bent 1940, Yanega unpubl. data). For Anna's Hummingbird the estimated mean hatching date was 6 March; for the Rufous it was 5 June. Thus, from hatching, we estimate the mean duration of bill smoothing (to 10% corrugation) in Anna's to be 234–242 days (7.5 to 8 months), and in the Rufous, 264–266 days (8.5 months).

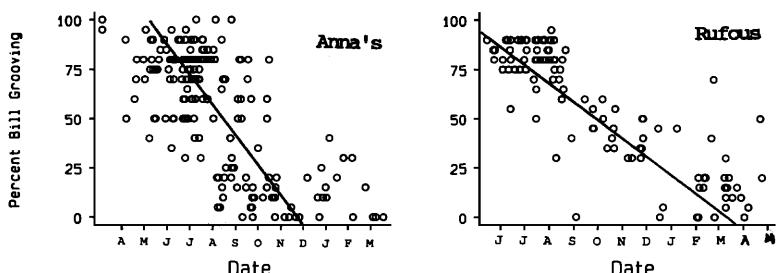


Figure 3. Corrugation proportions by month in first-year Anna's and Rufous Hummingbirds. Regression lines indicate the estimated smoothing rates for individuals.

BILL CORRUGATIONS FOR AGEING HUMMINGBIRDS

DISCUSSION

A potential problem with our banding data involves the use of multiple observers in scoring bill corrugation. Results from museum skins, scored primarily by Yanega, however, corroborate the banding records, although smaller proportions of adults were found with 5–10% bill corrugation. Many adults have small markings at the base of the bill that may or may not be equated with the corrugation found in juveniles (W. H. Baltosser, S. M. Russell pers. comm., pers. obs.). Other adults (approximately 20% of our museum specimens), however, do appear to retain up to 10% corrugation at the base of the bill. Similarly, W. H. Baltosser (pers. comm.) found that seven of 54 (13%) adult Black-chinned Hummingbirds (*Archilochus alexandri*) retained small amounts (<10%) of corrugation.

Our calculations of 7.5 to 8.5 months post-hatching (or 6.5 to 8.0 months post-fledging) for mean completion of bill smoothing (to 10% corrugation) should be used with discretion and, if possible, confirmed by study of marked birds in the field. On the basis of unquantified data from banded birds, Russell (1996) and W. H. Baltosser (pers. comm.) estimated completion of bill smoothing to be 5 to 6 months in most Anna's and Black-chinned hummingbirds, respectively. Our longer estimated completion rates could reflect biases in our corrugation estimates (particularly those of banded birds taken by multiple observers), imprecise estimates because of the wide variation in timing of the breeding seasons (especially for Anna's Hummingbird), and geographic or species-specific variation in the smoothing rates, resulting from differences in energetics, migratory strategy, and/or feeding behavior. Our data were taken mostly from populations of hummingbirds breeding in relatively cool and moist environments, where smoothing rates may be slowed by the higher energy demands for thermoregulation or, perhaps, the softer vegetation resulting in less bill wear. It is also possible that smoothing rates differ from year to year within a species (see Stiles 1973). Further quantitative study on corrugation in hummingbirds breeding in warmer and drier habitats could shed light on geographic and species-specific variation in bill-smoothing rates.

From our results, at least small proportions of first-year Anna's and Rufous hummingbirds can be distinguished by bill corrugation beyond the completion of first prebasic molts, typically by November in Anna's and by February in the Rufous (Williamson 1956, Calder 1993, Russell 1996, Pyle et al. in press). We conclude that birds with >10% corrugation can be reliably aged first-year in Anna's through at least mid-December (less frequently through January) and in the Rufous through at least mid-March (less frequently through mid-May). Birds with <10% corrugation can be reliably identified as adults through 20 September in Anna's and 30 January in Rufous. Consideration of plumage should always be combined with that of the bill corrugation in determining age of hummingbirds (Pyle et al. in press).

SUMMARY

In both Anna's and Rufous hummingbirds, a small percentage (13–20%) of adults retain up to 10% bill corrugation for at least 1.5 to 2 years.

BILL CORRUGATIONS FOR AGEING HUMMINGBIRDS

Regression analyses indicate that the mean time period in which young birds of both species reach 10% corrugation (at which time they cannot be aged by the bill) is 7.5 to 8.0 months from hatching in Anna's Hummingbird and 8.5 months from hatching in the Rufous Hummingbird. Although our calculated rates are somewhat imprecise and may be affected by geographic variation, we propose that at least a small proportion of first-year birds, with bill corrugation >10%, can be recognized as such up to two months beyond completion of the first prebasic molt.

ACKNOWLEDGMENTS

We thank the following for access and assistance to specimen collections: Karen Cebra and Luis Baptista (CAS), Kimball L. Garrett (LACM), John Hafner and James Northern (MLZ), Ned K. Johnson and Carla Cicero (MVZ), Philip Unit (SDNHM), and Walter Wehtje and Jon Fisher (WFVZ). We also acknowledge David F. DeSante for initiating the bill corrugation measurements at Palomarin, and the many volunteer banders who subsequently took the measurements. The manuscript was improved substantially by comments from W. H. Baltosser, S. M. Russell, and P. Unit. This is contribution 701 of PRBO.

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Accepted 8 November 1996