Short Communications and Commentaries

The Auk 111(3):703-710, 1994

Serrate Tomia: An Adaptation for Nectar Robbing in Hummingbirds?

JUAN FRANCISCO ORNELAS
Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA

Hummingbirds are distinguished from all other groups of birds by the range of bill-shape and bill-length variation. Such bill configurations are thought to match particular floral morphologies (e.g. Grant and Grant 1968, Stiles 1978, Brown and Kodric-Brown 1979, Stein 1992). Considerable research has been conducted on bill shape and length variation; in contrast, serrations have not received much attention. In their extensive review of the literature dealing with bills (and tongues) of nectarivorous birds, Paton and Collins (1989) make no mention of bill serrations. Bill serrations, a variable feature among hummingbirds, have been studied only in a few species. Only two genera, *Androdon* and *Ramphodon*, have been consistently reported as having bills with distinctly serrated edges (e.g. Ridgway 1890, 1911, Johnsgard 1983, Hilty and Brown 1986). According to Ridgway (1911), however, this character is present in other genera, and it consists of a variable number of minute serrations in the terminal portion of the maxillary and mandibular tomia. In this paper I describe bill serrations in hummingbirds at the generic level and discuss their functional significance.

Methods.—I studied skin collections at five museums (see Acknowledgments), examining skin specimens of 107 genera (98% of total of 110 genera) and 311 species (92% of total of 320 known species) of hummingbirds. I checked at least 10 specimens of each species for bill serrations using a stereomicroscope and/or a hand lens. Most museum skins are prepared with the mouth closed (often tied shut). When this was the case, I opened the bills carefully for examination. I recorded the following information: (1) shape of bill tip (e.g. hooked, wedge shaped); (2) the number and shape of serrations (when present); and (3) the distribution of the serrations along the bill (e.g. serrations only on maxillary tomium).

Results.—Twenty-eight genera (23% of hummingbird genera) have species with serrated bills (a total of 69 species; Figs. 1 and 2). Four of these genera also have hooked bill tips (Table 1). In the Tooth-billed Hummingbird (*Androdon aequatorialis*), both the upper and lower bill (maxilla and mandible) are hooked, and the edge of both tomia finely toothed (ca. 50 serrations along 10 mm) or fringed near the tip (Ridgway 1911, Johnsgard 1983; Fig. 1). The genera *Ramphodon, Glaucis*, and *Sappho* have hooked maxillas but straight or curved mandibles. Bill serrations are very conspicuous on both tomia in *Androdon* and *Ramphodon*, but in *Glaucis* and *Sappho* serrations were detected only on the maxillary tomium. The serrations are present only on one-third to one-half of the bill starting at the tip. Those toward the tip usually are longer and slant posteriorly at an angle of 45°.

In the 24 genera lacking hooked bill tips but having serrated tomia, the serrations at the tip of the bill are not as enlarged as in the previous group. Sixteen genera have serrations only on the maxillary tomium and 8 genera have serrations on both tomia (see Table 1).

Given the condition of many older specimens at museums, it was often impossible to count accurately the number of serrations. However, most genera have about 20 to 30 serrations along the cutting edge of the bill; serrations are most abundant distally and diminish proximally. A unique situation prevails in *Schistes geoffroyi* in which serrations were mainly observed at the middle of the bill. Individuals of *Androdon* and *Ramphodon* may have more than 50 very long and conspicuous serrations (Fig. 1). In *Chrysuronia, Cynanthus, Goldmania, Oreonympha, Taphrolesbia*, and in some species of *Chlorostilbon*, bill serrations are weakly developed when present (see Table 1). In such cases, the existence of serrate tomia must be regarded with uncertainty.

The shape of the bill is variable even among hummingbirds that lack a hooked tip. Most of the hummingbirds with serrations have very pointed bills. This very sharp cutting edge resembles a needle in *Doryfera, Augastes, Chrysolampis*, and *Damophila*. In two genera the terminal portion of the bill is very much compressed (i.e. wedge shaped; *Heliothryx* and *Augastes*; Ridgway 1911). The bill of the Fiery-tailed Awlbill (*Avocettula recurvirostris*) is upturned with serrations on both tomia (Fig. 1).

Discussion.—The parallel bill structures in *Androdon, Glaucis, Ramphodon*, and *Sappho* and 24 other genera have not been explored carefully. In the following sections, I propose two possible functional explanations for such morphological characteristics in hummingbirds.

It has been hypothesized that the function of bill serrations is to facilitate the holding of insects (Ridgway 1890, Johnsgard 1983, Hilty and Brown 1986,

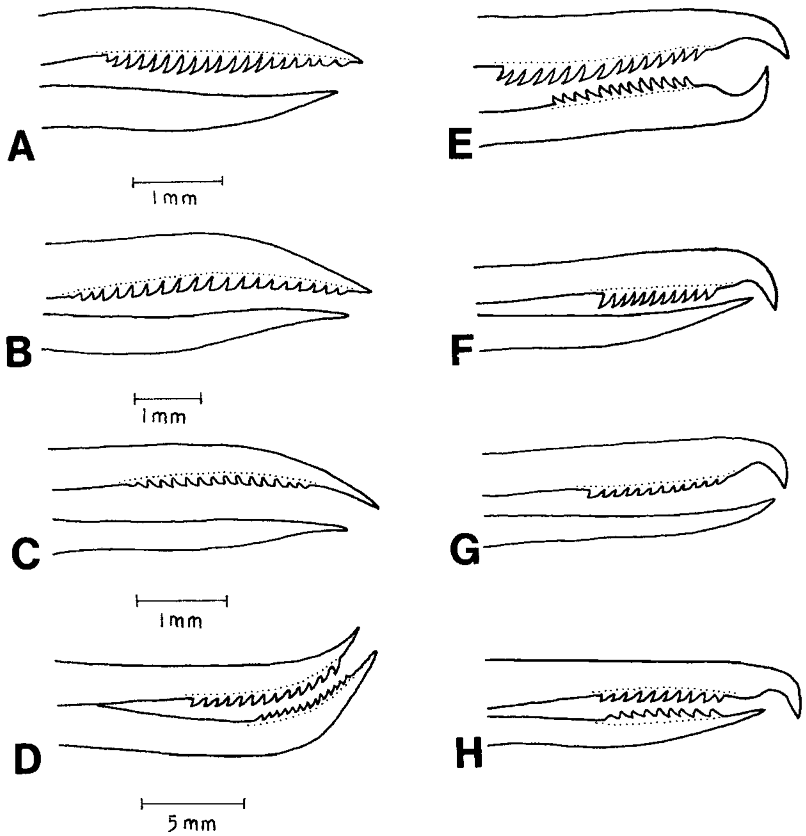

Fig. 1. Serrate tomia in lateral view. Drawings were made by examining several museum specimens (see Acknowledgments). **Left (unhooked bills):** (A) *Colibri coruscans;* (B) *Anthracothorax prevostii;* (C) *Thalurania furcata;* and (D) *Avocettula recurvirostris.* **Right (hooked bills):** (E) *Androdon aequatorialis;* (F) *Glaucis aenea;* (G) *Sappho shanganura;* and (H) *Ramphodon naevius.* Note changes in size (data available only for unhooked), shape, and orientation of serrations among species in both groups.

Gosner 1993). The hook and bill serrations may form part of a feeding structure of hummingbirds that specialize on hard-bodied arthropods. Such a morphological device may serve to secure prey by increasing the coefficient of friction when catching or holding prey.

Most hummingbirds routinely consume arthropods as a source of protein (Young 1971, Remsen et al. 1986, Chávez-Ramírez and Dowd 1992, Chávez-Ramírez and Tan 1993). Mobbs (1979) described five methods used in captivity among hummingbirds when capturing insects and attributed such variation to habitat differences (e.g. open areas vs. forest interiors) or to substrate (usually leaves or bark). Foraging techniques include flycatching and gleaning from flowers, leaves, and spider webs (Young 1971, Mobbs 1979). Two species with serrations on both tomia, the Green-throated Carib (*Sericotes holosericeus*) and Purple-throated Carib (*Eulampis jugularis;* Table 1), use different arthropod foraging methods (flycatching and flower gleaning, respectively) and forage in different habitats (open canopy and forest interior, respectively; Chávez-Ramírez and Dowd 1992, Chávez-Ramírez and Tan 1993). This suggests that an association of bill serrations with foraging technique and/or habitat type is unlikely.

Little is known about how hummingbirds handle different types of arthropod prey. In aviaries, hummingbirds seem incapable of manipulating prey items with the bill or even holding them for more than a few seconds (pers. obs., Thompson 1974). Mobbs (1979) observed that "when a hummer captures an insect in flight (hawking), its forward movement forces the prey so far to the rear of the gape that it is already swallowed." It is possible, however, that highly insectivorous hummingbirds use the bill serrations for manipulating food items.

Gosner (1993) suggested that scopate tomia in birds (i.e. brushlike ridges on cutting edges of mandibles) are adaptations for handling hard-shelled prey. If this is true, one would expect that hummingbirds with serrated bills should feed on aerial hard-bodied prey.

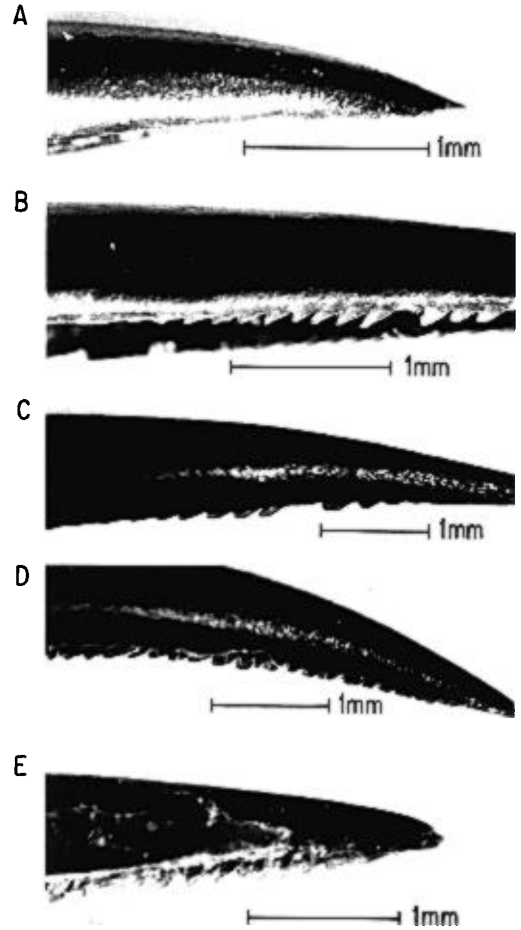

Fig. 2. Photographs showing only upper mandibles. **Smooth tomia:** (A) *Campylopterus hemileucurus* (UA, 8 972). **Serrate tomia:** (B) *Colibri coruscans* (UA, 13 897); (C) *Thalurania ridgwayi* (UA, 8 025); (D) *Anthracothorax prevostii* (UA, 13 010); and (E) *Colibri coruscans* (UA, 13 898).

Table 1. Genera of hummingbirds with minute serrations on tomia.

Genera	Hook	Serrations Only maxilla	 Both tomia	Known to rob nectar
Aglaiocercus		X		
Androdon	X		X	
Anthracothorax		X		X
Augastes		X		
Avocettula			X	
Chalybura			X	
Chlorostilbon		X		X
Chrysolampis			X	
Chrysuronia		X[a]		
Colibri		X		X
Cynanthus		X[a]		
Damophila			X	
Doryfera			X	
Elvira		X		
Eulampis			X	X
Eupherusa		X		X
Glaucis	X	X		
Goldmania		X[a]		
Heliothryx		X		X
Polytmus			X	
Oreonympha		X[a]		
Ramphodon	X		X	
Sappho	X	X		
Sericotes			X	X
Schistes		X		
Taphrolesbia		X[a]		
Thalurania		X		X
Trochilus		X		X

[a] Serrate tomia, when present, weakly developed (see text).

Hummingbirds with a hook and/or serrations on their bills would be capturing and holding different types of prey and using different foraging techniques (e.g. gleaning vs. flycatching) than birds without hooks or serrations on their bills. Little is known about the types of arthropods hummingbirds consume, but Remsen et al. (1986) found that hermits take a much higher proportion of soft-bodied spiders than do most nonhermits. Based on this possible pattern, one would expect to find bill serrations distributed mostly among nonhermit species. This seems not to be the case. According to the classification of Sibley and Monroe (1990), 25% of the genera in each group of hummingbirds have serrated bills (6.8% of all hermit species and 23.1% of all nonhermit species).

There is no evidence then that, among either group of hummingbirds, those with serrated bills specialize on hard-bodied arthropods, nor that when hummingbirds forage they use consistently the same technique and/or forage on the same substrata. A detailed study is needed of the kind of arthropods consumed by both hermits and nonhermits. The arthropod-feeding hypothesis for serrate tomia and hooked bills can be evaluated as information accumulates on (1) differences in arthropod diets of hummingbirds, and (2) differences in arthropod-foraging techniques.

Nectar robbing is a behavior exhibited by various species of hummingbirds and passerine birds. Nectar is obtained through holes made near the bases of the corolla tubes, in a manner generally circumventing contact with the sexual parts of the flowers (Inouye 1983). I hypothesize that bill serrations may enhance the exploitation of resources such as long-tubed corollas and tough-tissue corollas by facilitating: access to protected nectaries; the grasping of tough and waxy blooms; and the cutting of flower tissue.

There are several morphological similarities between passerine flower-piercers (*Diglossa*) and the hummingbirds that have serrate tomia. The maxilla of a typical species of *Diglossa* sweeps slightly upwards from its base and ends in a distinct strong hook

TABLE 2. Nectar robbing in the family Trochilidae and plants utilized by nectar-robbing hummingbirds.

Hummingbird species	Plant species (reference[a])
	Primary nectar robbers
Anthracothorax nigricollis	*Tabebuia serratifolia* (3)
A. viridis	*Malvaviscus arboreus* (9)
Chlorostilbon maugaeus	*Erythrina berteroana* (9), *Neurodolphia volubilis* (5), *Malvaviscus arboreus* (9), *Pitcairnia angustifolia* (9), *P. bromeliifolia* (5), *Tabebuia haemantha* (5), *T. rigida* (9), *T. schumanniana* (5)
C. mellisugus	Plant not identified (7)
C. ricordii	*Barlena cristata* (9), *Tabebuia rosea* (9)
Colibri thalassinus	*Salvia* spp. (8)
Eulampis jugularis	Plant not identified (9)
Eupherusa eximia	Plant not identified (13), *Justicia aurea* (2), *Malvaviscus palmarus* (2), *Drymonia rubra* (2), *Drymonia conchocalyx* (2), *Razisea spicata* (2), *Poikilacanthus macranthus* (2)
Heliothryx barroti	*Erythrina* sp. (10), *Aphelandra golfodulcensis* (6), *Razisea* sp. (12), *Heliconia* spp. (13)
Thalurania ridgwayi	Plant not identified (8)
Trochilus polytmus	Plant not identified (9)
	Secondary nectar robbers
Panterpe insignis	Plant not identified (11), *Centropogon talamancensis* (1)
	Nectar thieves
Calliphlox evelynae	Plant not identified (9)
Heliodoxa jacula	*Marcgravia* spp. (12)
Lesbia sp.	*Brugmansia* sp. (4)
Phaethornis longuemareus	Plant not identified (14), *Aphelandra golfodulcensis* (6), *Justicia aurea* (6)
Selasphorus flammula	*Centropogon valerii* (1)
Threnetes ruckeri	*Calathea* spp. (13)

[a] References: (1) Colwell et al. 1974; (2) Feinsinger et al. 1987; (3) ffrench 1973; (4) Gould 1861; (5) Kodric-Brown et al. 1984; (6) McDade and Kinsman 1980; (7) Meyer de Schauensee and Phelps 1978; (8) pers. obs.; (9) Quesada-Tyrrell and Tyrrell 1990; (10) Skutch 1973; (11) Stiles 1983; (12) Stiles 1985; (13) Stiles and Skutch 1989; (14) Wetmore 1968.

(Vuilleumier 1969, Bock 1985) as in *Androdon, Glaucis, Ramphodon,* and *Sappho.* Immediately behind the hook, there is a notch in the maxillary tomium that is followed by two to four serrations in *Diglossa* (but these are weak or almost absent in some species; Bock 1985). Similarly, among hummingbirds, 28 genera have the edge of the tomia finely toothed near the tip, so that the tip of the bill resembles that of a flower-piercer bill (pers. obs., Ridgway 1890).

The hook and serrations of the upper jaw, the flat cutting edge of the mandibular tip, and the incomplete mandibular tube in *Diglossa* species are all parts of a specialized adaptive complex associated with the unusual method of nectar feeding used by flower-piercers (Bock 1985). The bird robs nectar first by holding the side of the flower with its hooked upper jaw and cutting through the corolla wall with the mandibular tip. With the corolla held in place, a longitudinal slit is cut into its near wall with the mandibular tip. Finally, the bird's tongue is protruded through this slit into the flower to obtain nectar (Skutch 1954, Vuilleumier 1969).

The *Diglossa* flower-piercers are perhaps the best-known examples of nectar robbers among birds (Skutch 1954, Lyon and Chadek 1971, Colwell et al. 1974, Snow 1981, Kodric-Brown et al. 1984, Arizmendi 1994), but several studies have reported flower piercing by short-billed hummingbirds (Beal 1880, Ridgway 1890, Grant 1952, Skutch 1954, Colwell 1973, Gentry 1974, Janzen 1975, Ingels 1976, Feinsinger and Colwell 1978, Snow 1981, Inouye 1980a, 1983; for more references, see Table 2).

Four behavioral categories among nectar robbers can be recognized (after Inouye 1980b): (1) highly specialized primary nectar robbers perforate the base of long-tubed corollas (gamepetalous corollas) pollinated mainly by other hummingbirds; (2) secondary nectar robbers utilize flowers perforated by other hummingbirds or passerine flower-piercers; (3) nectar thieves use the opening utilized by pollinators but, without biting or making holes, collect nectar from flowers morphologically adapted for pollination by a different class of visitors; and (4) base workers obtain nectar by reaching between the petals. This behavior is performed to flowers with polypetalous corollas, thereby bypassing the opening used by pollinators and gaining more direct access to the nectary at the base of the corolla. For example, Chávez-Ramírez and Dowd (1992) observed Dominican caribs probing between the petals (polypetalous corolla) to take nectar. The observation indicates that caribs, which have serrated tomia, fit the definition of base workers (after Inouye 1980b); however, caribs also exhibit behaviors of a nectar thief, as observed by Ingels (1976). According to Inouye (1980b), however, a base worker would not cut the flowers with its bill, but the opening used by pollinators is not used either. Caribs apparently do not cut the flowers with their bills, but would be better able to probe between petals due to the serrated tomia on their bills. Sometimes these hummingbirds would collect nectar that has leaked between the petals.

Some primary nectar robbers (after Inouye 1983) are mostly referred to in the literature as "marauders" (see Feinsinger and Colwell 1978), and secondary nectar robbers and nectar thieves are considered as parasitoids. However, I follow the categorization made by Inouye (1980b) to minimize confusion. Because nectar thieves probably do not greatly influence the activities of pollinators (Inouye 1980b, Stiles 1985), I do not include them in further discussion.

Hummingbirds exert strong selective pressures on corolla morphology. For example, Fenster (1991) suggested that corolla length is a floral specialization due to competition for pollinators. By increasing corolla length, plants are discriminating among a set of pollinators (i.e. long-billed hummingbirds) that would evolve as highly specialized on commonly rich-nectar, long-tubed corollas (e.g. Wolf et al. 1976).

Once a mutualistic relationship has arisen, there is a high probability that a third species might evolve to take advantage of mutualistic partnerships (Boucher et al. 1982, Inouye 1983, Soberón and Martínez del Rio 1985). Nectar robbers are probably the best-documented example of cheating behavior (Soberón and Martínez del Rio 1985) deriving benefits from flowers without pollinating, while competing with the pollinators for nectar (McDade and Kinsman 1980, Arizmendi 1994). Some hummingbird flowers are structurally protected against nectar robbers (Inouye 1980b), but most are unprotected and are regularly exploited by nectar robbers, which significantly affect the amount of nectar available to the pollinators (Snow 1981, Arizmendi 1994). However, the ecological impact of nectar robbing on both plant reproductive fitness and pollinators' foraging efficiency remains controversial (Hawkins 1961, Heinrich and Raven 1972, Koeman-Kwak 1973, McDade and Kinsman 1980, Soberón and Martínez del Rio 1981, Roubik 1982, Inouye 1983, Kodric-Brown et al. 1984, Arizmendi 1994).

It has been assumed that short-billed hummingbirds cannot feed on flowers with long corollas (Colwell et al. 1974), but these species often obtain nectar from flowers with long corollas by making perforations at the base (Darwin 1889, Skutch 1973). This behavior indicates that flowers with long corollas secrete nectar attractive to short-billed hummingbirds so long as they are able to extract it (e.g. Kodric-Brown and Brown 1979, Inouye 1983, Kodric-Brown et al. 1984, Feinsinger et al. 1987). Hummingbirds may pierce the base of flowers with long corollas with a short, serrate, hooked, and/or exceptionally sharp bill. An obvious prediction is that serrated tomia should be more prevalent among short-billed hummingbirds than long-billed hummingbirds.

There are several immediate benefits to the cheater when it performs this behavior. First, nectar robbing is potentially more energy efficient than legitimate flower visitation (Darwin 1889). Furthermore, it has been demonstrated with bees that the cost of foraging decreases if nectar is obtained by circumventing the flower entrance (Weaver 1956, Free 1968, Inouye 1980a; but see Soberón and Martínez del Rio 1985). Second, nectar robbers have access to highly rich resources (i.e. nectar in long-tubed corollas) that otherwise are restricted only to long-billed pollinators. This behavior is advantageous to nectar robbers when their legitimate access to nectar in short-tubed corollas is restricted (e.g. by competition, or by scarcity of accessible flowers).

One trade-off for being opportunistic (i.e. obtaining nectar by bypassing the opening used by pollinators) is rarity (Brian 1957, Stiles 1975, Kodric-Brown and Brown 1979, Soberón and Martínez del Rio 1985). Individuals of a third species take advantage of mutualistic partnerships and become density dependent on the mutualistic interaction. Rarity among nectar robbers would be the evolutionary outcome of plant specialization on a particular set of true pollinators (e.g. long-billed hummingbirds) and the improvement of the robbing techniques of the excluded nectar exploiters (i.e. hummingbirds with short, serrated bills). As predicted, nectar-robbing hummingbirds seem to be rare in nature (Stiles 1985, Hilty and Brown 1986) and/or erratic on a regional scale. When present at a smaller scale, however, nectar robbers are fairly common (pers. obs., Stiles 1985, Hilty and Brown 1986, Feinsinger et al. 1987, Collar et al. 1992, Ornelas in press).

Since nectar robbing lets the nectar exploiter become essentially independent of floral morphology (Stiles 1985), some behavioral attributes should be associated with this behavior. For example, Stiles (1983) observed that Fiery-throated Hummingbirds (*Panterpe insignis*) utilize flowers perforated by passerine flower-piercers and may follow the flower-piercer from flower to flower, using the flower-piercers' holes to extract the nectar. This observation suggests that an inherent difference in behavior should exist between this nectar robber and a nonnectar-robbing species (Brian 1957). In contrast to most hummingbirds that visit flowers by the obvious and correct entrance, nectar robbers should be expected to have a more plastic and less stereotyped set of behaviors. In contrast to most legitimate visitors, nectar robbers need to keep track of the flowers that have been punctured by the flower-piercers and have to deal with, for example, flowers with well-protected nectaries such as most bromeliads. This suggests that nectar robbers should differ from legitimate visitors in their tenacity and observational skills when obtaining food. Another difference between these two groups of hummingbirds is that individuals of most nectar robbers forage alone, and rarely defend territories (Wetmore 1968, ffrench 1973, Meyer de Schauensee and Phelps 1978, Stiles 1985, Hilty and Brown 1986, Stiles and Skutch 1989). Typically, nectar robbers do not establish territories, but they are notably bellicose; they are able to withstand attacks of most territorial hummingbirds (Stiles 1985, Stiles and Skutch 1989).

The rhamphothecal features of the flower-piercers are adaptations for nectarivory on flowers with long corollas (Bock 1985). However, the flower-piercing method of nectar feeding on flowers with deep corollas is not restricted to the flower-piercers among passerines, but is found in two other genera (*Coereba* and *Conirostrum*) and in several genera of hummingbirds (e.g. Skutch 1954, Bock 1985, Stiles and Skutch 1989; see Table 2). This suggests that the complex of features of the bill for nectar robbery has evolved more than once in birds with such morphology. Although a phylogeny of the Trochilidae is not yet available, the existence of serrated tomia in otherwise dissimilar hummingbird species leads me to suggest that this feature has evolved several times independently within the family.

With the evidence presented above, it appears that bill serrations are an adaptation in some hummingbirds for nectar robbing, but further support for this idea is required from ontogenetic, phylogenetic, and behavioral studies.

Acknowledgments.—I thank Felipe Chávez-Ramírez, W. Mark Roberts, Gary D. Schnell, and Larry L. Wolf for helpful discussion and review of the manuscript. Lucinda McDade, Stephen M. Russell, Peter Scott, Susan Wethington, and Yaron Ziv provided invaluable suggestions concerning earlier versions of the manuscript. I thank the following curators for allowing me to examine specimens under their care: G. Barrowclough (American Museum of Natural History, AMNH); P. Escalante and L. Navarijo (Colección Ornitológica del Instituto de Biología de la Universidad Autónoma de México, IBUNAM); T. Huels (University of Arizona, UA); A. Navarro (Museo de Zoología de la Facultad de Ciencias de la Universidad Autónoma de México, MZFC); and A. T. Peterson and D. Willard (Field Museum of Natural History, FMNH). Kris Sonderegger prepared the illustration. Funding was provided by scholarship 56254 from Consejo Nacional de Ciencia y Tecnología (CONACyT-México), and by a grant from the University of Arizona Research Training Group (RTG) in the Analysis of Biological Diversification.

LITERATURE CITED

ARIZMENDI, M. C. 1994. Interacciones ecológicas múltiples: El caso del sistema mutualista colibríes-plantas y el ladrón de néctar *Diglossa baritula* (Passeriformes: Aves). Tesis Doctorado, Univ. Nacional Autónoma de México, México, D.F.

BEAL, W. J. 1880. Fertilization of flowers by hummingbirds. Am. Nat. 14:126–127.

BOCK, W. J. 1985. Is *Diglossa* (?Thraupinae) monophyletic? Pages 319–332 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. 36.

BOUCHER, D. H., S. JAMES, AND K. H. KEELER. 1982. The ecology of mutualism. Annu. Rev. Ecol. Syst. 13:315–347.

BRIAN, A. D. 1957. Differences in the flowers visited by four species of bumblebees and their causes. J. Anim. Ecol. 26:71–98.

BROWN, J. H., AND A. KODRIC-BROWN. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. Ecology 60:1022–1035.

CHÁVEZ-RAMÍREZ, F., AND M. DOWD. 1992. Arthropod feeding by two Dominican hummingbird species. Wilson Bull. 104:743–747.

CHÁVEZ-RAMÍREZ, F., AND S. S. TAN. 1993. Habitat separation and arthropod resource use in three Lesser Antillean hummingbirds. Condor 95:455–458.

COLLAR, N. J., L. P. GONZAGA, N. KRABBE, A. MADROÑO NIETO, L. G. NARANJO, T. A. PARKER III, AND D. C. WEGE. 1992. Threatened birds of the Americas. The ICBP/IUCN red data book, 3rd ed., part 2. International Council for Bird Preservation, Cambridge, United Kingdom.

COLWELL, R. K. 1973. Competition and coexistence in a simple tropical community. Am. Nat. 107: 737–760.

COLWELL, R. K., B. J. BETTS, P. BUNNELL, F. L. CARPENTER, AND P. FEINSINGER. 1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalassinus* and the flower-piercer *Diglossa plumbea*, and its evolutionary implications. Condor 76:447–452.

DARWIN, C. 1889. The effects of cross and self-fertilization in the vegetable kingdom. D. Apleton, New York.

FEINSINGER, P., AND R. K. COLWELL. 1978. Community organization among Neotropical nectar-feeding birds. Am. Zool. 18:779–795.

FEINSINGER, P., J. H. BEACH, Y. B. LINHART, W. H. BUSBY, AND G. MURRAY. 1987. Disturbance, pollinator predictability, and pollination success among Costa Rican cloud forest plants. Ecology 68:1294–1305.

FENSTER, C. B. 1991. Selection on floral morphology by hummingbirds. Biotropica 23:98–101.

FFRENCH, R. 1973. A guide to the birds of Trinidad and Tobago. Livingston Publishing Co., Wynnewood, Pennsylvania.

FREE, J. B. 1968. The behavior of bees visiting runner beans (*Phaseolus multiflorus*). J. Appl. Ecol. 5:631–638.

GENTRY, A. H. 1974. Coevolutionary patterns in Central American Bignoniaceae. Ann. Missouri Bot. Garden 61:728–759.

GOSNER, K. L. 1993. Scopate tomia: An adaptation for handling hard-shelled prey? Wilson Bull. 105: 316–324.

GOULD, J. 1861. Introduction to the Trochilidae or family of humming-birds. Printed (for the author) by Taylor and Francis, London, United Kingdom.

GRANT, V. 1952. Isolation and hybridization between *Aquilegia formosa* and *A. pubescens.* Aliso 2:341–360.

GRANT, K. A., AND V. GRANT. 1968. Hummingbirds and their flowers. Columbia Univ. Press, New York.

HAWKINS, R. P. 1961. Observations on the pollination of red clover by bees: I. The yield of seeds in relation to numbers and kinds of pollinators. Ann. Appl. Biol. 49:55–65.

HEINRICH, B., AND P. H. RAVEN. 1972. Energetics and pollination ecology. Science 176:597–602.

HILTY, S. L., AND W. L. BROWN. 1986. A guide to the birds of Colombia. Princeton Univ. Press, Princeton, New Jersey.

INGELS, J. 1976. Observations on the hummingbirds *Orthorhynchus cristatus* and *Eulampis jugularis* of Martinique (West Indies). Gerfaut 66:129–132.

INOUYE, D. W. 1980a. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation. Oecologia 45:197–201.

INOUYE, D. W. 1980b. The terminology of floral larceny. Ecology 61:1251–1253.

INOUYE, D. W. 1983. The ecology of nectar robbing. Pages 153–173 *in* The biology of nectaries (B. Bentley and T. Elias, Eds.). Columbia Univ. Press, New York.

JANZEN, D. H. 1975. Ecology of plants in the tropics. Edward Arnold, London.

JOHNSGARD, P. A. 1983. The hummingbirds of North America. Smithsonian Institution Press, Washington, D.C.

KODRIC-BROWN, A., AND J. H. BROWN. 1979. Competition between distantly related taxa in the coevolution of plants and pollinators. Am. Zool. 19: 115–127.

KODRIC-BROWN, A., J. H. BROWN, G. S. BYERS, AND D. F. GORI. 1984. Organization of a tropical island community of hummingbirds and flowers. Ecology 65:1358–1368.

KOEMAN-KWAK, M. 1973. The pollination of *Pedicularis pallustris* by nectar thieves (short-tongued bumblebees). Acta Bot. Neederlandica 22:608–615.

LYON, D. L., AND C. CHADEK. 1971. Exploitation of nectar resources by hummingbirds, bees (*Bombus*), and *Diglossa baritula* and its role in the evolution of *Penstemon kunthii.* Condor 73:246–248.

MCDADE, L. A., AND S. KINSMAN. 1980. The impact of floral parasitism in two Neotropical hummingbird-pollinated plant species. Evolution 34: 944–958.

MEYER DE SCHAUENSEE, R., AND W. H. PHELPS. 1978. A guide to the birds of Venezuela. Princeton Univ. Press, Princeton, New Jersey.

MOBBS, A. J. 1979. Methods used by the Trochilidae when capturing insects. Avic. Mag. 85:26–30.

ORNELAS, J. F. In press. Capítulo II. Las especies extintas y amenazadas sección 2. Aves:familia Trochilidae. *In* Vertebrados Mexicanos extintos y en peligro de extinción (G. Ceballos and D. Navarro, Eds.). Univ. Nac. Autón. Méx., México, D.F.

PATON, D. C., AND B. G. COLLINS. 1989. Bills and tongues of nectar-feeding birds: A review of morphology, function and performance, with intercontinental comparisons. Aust. J. Ecol. 14:473–506.

QUESADA-TYRRELL, E., AND R. A. TYRRELL. 1990. Hummingbirds of the Caribbean. Crown Publishers, New York.

REMSEN, J. V., F. G. STILES, AND P. E. SCOTT. 1986. Frequency of arthropods in stomachs of tropical hummingbirds. Auk 103:436–441.

RIDGWAY, R. 1890. The hummingbirds. Rep. Am. Mus. Nat. Hist., New York.

RIDGWAY, R. 1911. The Birds of North and Middle America, part 5. Smithsonian Institution Press, Washington, D.C.

ROUBIK, D. W. 1982. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. Ecology 63:354–360.

SIBLEY, C. G., AND B. L. MONROE. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, London.

SKUTCH, A. F. 1954. Life histories of Central American birds, vol. 1. Pacific Coast Avifauna Series 31.

SKUTCH, A. F. 1973. The life of the hummingbird. Crown Press, New York.

SNOW, D. W. 1981. Coevolution of birds and plants. Pages 169–178 *in* The envolving biosphere (P. J. Greenwood, Ed.). Cambridge Univ. Press, Cambridge.

SOBERÓN, J., AND C. MARTÍNEZ DEL RIO. 1981. The dynamics of a plant-pollinator interaction. J. Theor. Biol. 91:363–378.

SOBERÓN, J., AND C. MARTÍNEZ DEL RIO. 1985. Cheating and taking advantage in mutualistic associations. Pages 192–216 *in* The biology of mutualism (D. H. Boucher, Ed.). Croom Helm, London.

STEIN, B. A. 1992. Sicklebill hummingbirds, ants, and flowers. Bioscience 42:27–33.

STILES, F. G. 1975. Ecology, flowering phenology and hummingbird pollination of some Costa Rican *Heliconia* species. Ecology 56:285–301.

STILES, F. G. 1978. Ecological and evolutionary implications of bird pollination. Am. Zool. 18:715-727.

STILES, F. G. 1983. Species accounts. Birds. Pages 593-594 *in* Costa Rican natural history (D. H. Janzen, Ed.). Univ. Chicago Press, Chicago.

STILES, F. G. 1985. Seasonal patterns and coevolution in the hummingbird-flower community of a Costa Rican subtropical forest. Pages 757-787 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. 36.

STILES, F. G., AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell Univ. Press, Ithaca, New York.

THOMPSON, A. L. 1974. A new dictionary of birds. McGraw-Hill, New York.

VUILLEUMIER, F. 1969. Systematics and evolution in *Diglossa* (Aves, Coerebidae). Am. Mus. Novit. 2381.

WEAVER, N. 1956. The foraging behavior of honeybees on hairy vetch. I. Foraging methods and learning to forage. Insects Sociaux 3:547-549.

WETMORE, A. 1968. The birds of the Republic of Panama. Smithson. Misc. Coll., vol. 150, part 2.

WOLF, L. L., F. G. STILES, AND F. R. HAINSWORTH. 1976. Ecological organization of a tropical highland hummingbird community. J. Anim. Ecol. 45:349-379.

YOUNG, A. M. 1971. Foraging for insects by a tropical hummingbird. Condor 73:36-45.

Received 2 December 1993, accepted 22 January 1994.

The Auk 111(3):710-713, 1994

Divergence in the Mitochondrial DNA of *Empidonax traillii* and *E. alnorum*, with Notes on Hybridization

KEVIN WINKER[1]

Academy of Natural Sciences, Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103, USA

The *Empidonax* flycatchers represent a morphologically conservative species assemblage. This conservatism has made recognition of species limits difficult, and there has been a recent trend toward recognizing separate species among populations formerly considered conspecific (e.g. Stein 1958, 1963, Johnson 1980, Johnson and Marten 1988). *Empidonax* flycatchers represent a group where molecular systematics can address a variety of heretofore unanswered questions, especially those regarding degrees of distinctiveness and gene flow between populations or species (see also Hewitt 1988, Avise and Ball 1991). Sibling species such as the Willow Flycatcher (*E. traillii*) and Alder Flycatcher (*E. alnorum*) are particularly interesting with regard to the evolution of intrinsic isolating mechanisms, an important component of the speciation process. The degree to which intrinsic reproductive isolating mechanisms (i.e. ability to discriminate between con- and heterospecifics, resulting in assortative mating) have arisen between two allopatric populations will affect how distinct these gene pools will remain following secondary contact.

A scarcity of recognized hybrids among *Empidonax* flycatchers suggests that, although they are morphologically conservative, their intrinsic reproductive isolating mechanisms (or cohesion mechanisms; Templeton 1989) are remarkably well developed. Perhaps, however, it is our inability to recognize *Empidonax* hybrids, rather than their true rarity, that leads to their apparent scarcity. Two of the five recognized tyrannid hybrids (see Short and Burleigh 1965, Phillips 1966, Phillips and Short 1968) are intergeneric, suggesting that congeneric hybrids are being overlooked. Further, because individuals of the genus *Empidonax* (including *E. traillii*) have produced hybrids with heterospecifics (see Short and Burleigh 1965, Phillips 1966), hybridization might be predicted between the closely related *E. traillii* and *E. alnorum.* Seutin and Simon (1988) arrived at the same conclusion in a different manner, suggesting that the close phenotypic similarity and habitat preferences of *E. alnorum* and *E. traillii,* together with the extensive zone of sympatry, makes hybridization between them likely. These authors failed to find evidence of hybridization, however, and concluded that these species were reproductively isolated in southeastern Canada. They sought evidence of hybridization using allozyme electrophoresis, although this technique had already revealed no fixed allelic differences between the two species in Minnesota (Zink and Johnson 1984). Without a fixed-allelic difference, the ability to detect hybrids is compromised. Another problem with the study was that it did not include *traillii* from allopatric populations.

My study consisted of three parts: (a) estimating the level of divergence in the mitochondrial DNA (mtDNA) of *E. traillii* and *E. alnorum;* (b) finding spe-

---

[1] Present address: National Museum of Natural History, Division of Birds, Smithsonian Institution, Washington, DC 20560, USA.