6-27-2018

Rivoli's Hummingbird: Eugenes fulgens

Donald R. Powers
George Fox University, dpowers@georgefox.com

Rivoli's Hummingbird

Eugenes fulgens

Order: CAPRIMULGIFORMES
Family: TROCHILIDAE
Version: 2.1 — Published June 27, 2018
Donald R. Powers

Introduction

Rivoli's Hummingbird was named in honor of the Duke of Rivoli when the species was described by René Lesson in 1829 (1). Even when it became known that William Swainson had written an earlier description of this species in 1827, the common name Rivoli's Hummingbird remained until the early 1980s, when it was changed to Magnificent Hummingbird. In 2017, however, the name was restored to Rivoli's Hummingbird when the American Ornithological Society officially recognized *Eugenes fulgens* as a distinct species from *E. spectabilis*, the Talamanca Hummingbird, of the highlands of Costa Rica and western Panama (2). See Systematics: Related Species.

Rivoli's Hummingbird is found from the southwestern United States to northern Nicaragua, and is the second-largest hummingbird species in the United States. It exhibits sexual dimorphism, primarily in coloration, body mass, and bill length. The species typically occurs at middle to high elevations throughout much of Mexico and Central America. Birds migrate north in early spring to breed, some of them reaching forested mountains at the northern limit of the breeding range in Arizona and New Mexico. Throughout its range, Rivoli's Hummingbird occurs in a variety of habitats, but it is most frequently found in dry pine–oak (*Pinus–Quercus*) forests. Breeding is often associated with cool canyons and drainages in the mountain ranges of southern Arizona and New Mexico, where nests are often constructed high up in trees that overhang streams.

Despite the extensive range and abundance of the Rivoli's Hummingbird, its basic life history is largely unknown, with most information coming from studies in central and southern Mexico. The transient nature of males and the secretive habits of females have made research in the U.S. difficult, although it appears that northern males may forage more by traplining (see Behavior: Agonistic Behavior) than by being territorial and aggressive. Additional information is needed on migration and movement ecology,

breeding biology (courtship, nest construction, number of broods, nestling development, parental care), breeding success, feeding behavior (dietary importance of insects; role of bill dimorphism in feeding efficiency), and the function of vocalizations.

Appearance

Second-largest hummingbird in North America (typically 7.5–8.5 g, 11–13 cm). Head large relative to body size; bill black, long (up to 30 mm), and stout, straight tail slightly notched. Male slightly larger, shorter billed, and more brightly colored than female. Male has iridescent purple crown, iridescent green gorget, small white spot behind eye, black underparts, and dark green upperparts with metallic bronze, bronze green, or golden green coloration in large feathers of wing and tail. Adult female also has a small white spot behind eye and a dark green back, but lacks iridescent coloration on head and bronze coloration on wings and tail, and has lighter underparts. Juveniles resemble adult female, with first-year males gaining partial adult-like plumage during the partial preformative molt. Outer 2–4 rectrices of juveniles and adult females with small white tip, which often become worn off or grayish and duller in appearance; rectrices of adult males usually lack white.

Similar Species

Black underparts, unique among North American hummingbirds, cause male to appear very dark. Large size and all-black bill distinguish Magnificent from other North American hummingbirds. Large head and long bill generally distinguish this species from Blue-throated Hummingbird(*Lampornis clemenciae*), a sympatric species in southwestern U.S. and Mexico of similar size, when coloration is difficult to see. Female Rivoli's Hummingbird may also be confused with female Blue-throated Hummingbird, but female Blue-throated has wider blue-black rectrices with large, white distal patches, a well-defined supercilium extending well behind eye, and nares uncovered by feathers, whereas the rectrices of female Rivoli's Hummingbird are narrower and mostly green and gray, with small white or grayish tips, the supercilium is reduced to a post-ocular spot, and the fetahers of the forehead extend down the bill to cover the nares. Forked tail and absence of white stripe on rump distinguish Rivoli's Hummingbird from Long-billed Starthroat(*Heliomaster longirostris*) and Plain-capped Starthroat (*H. constantii*).

Detailed Description

Rivoli's Hummingbird has 10 full-length primaries (numbered distally, p1 to p10), 6 secondaries (numbered proximally, s1 to s6), and 10 rectrices (numbered distally, r1 to r5, on each side of the tail). Little or no geographic variation in appearance (see Systematics: Geographic Variation) or geographic or sex-specific variation molt strategies reported within North America, although some variation in average timing and extent occurs with latitude of breeding through Mexico and northern Central America, responding to variable environmental and migratory constraints, day-length regimes, and breeding seasonality (*cf.* 3).

Plumages

See Molts for molt and plumage terminology; plumage strategies revised from those previously reported based on re-examination of specimens at the Museum of Vertebrate Zoology (MVZ) and California Academy of Sciences (CAS) by P. Pyle. The following are based primarily on detailed plumage descriptions of Ridgway (4), Oberholser (5), Howell (6), and Williamson (7); see Pyle (8) for specific age/sex-related criteria. Sexes of Juveniles differ slightly in appearance, by rectrix pattern, while those in subsequent plumages are marked. Definitive appearance assumed at Second Basic Plumage. Color terminology largely from Ridgway (4).

Natal Down

Natal down reportedly absent (5), but confirmation needed.

Juvenile (First Basic) Plumage

Present primarily May–August in North American populations. Similar to Definitive Basic female (below) but upperpart feathers duller olive and narrowly margined terminally with pale grayish buff; underparts slightly darker and variably suffused pale brownish buff. Body plumage similar in juvenile **Female** and **Male** (*cf*. 9); reports of Juvenile males with partial definitive-male appearance presumably based on individuals in Formative Plumage (see below). Sexes only differ by pattern to rectrices (more white to tips of outer three pairs in females than in males), as described under Formative and Definitive Basic Plumages (below).

Formative Plumage

"First Basic" or "Basic I" plumage of Humphrey and Parkes (10) and later authors; see revision by Howell et al. (11) and Molts. Present primarily June-second August in North American populations; plumage in transitional state during much or all of this period due to protracted Preformative Molt.

Male. Similar to Juvenile Plumage but increasingly (from July–April) appearing like Definitive male; forehead, auriculars, nape, and breast increasingly blackish; mid-crown with increasingly iridescent dark bluish to violet; upperparts increasingly brighter green, the feathers without grayish fringes; throat increasingly iridescent green; rectrices as in Definitive Basic male but with broader, diffuse off-white tips to lateral pairs; upperwing coverts duller green, some lesser coverts sometimes replaced, contrastingly brighter green. Progression of Formative male plumage shown by specimens collected in Arizona: MVZ 11835 (13 July 1896) and CAS 75376 (5 July 1893) with fresh juvenile flight-feathers but incoming iridescent green gorget feathers and black underpart feathers), and MVZ 78796 (7 June 1894), and CAS 58904 (19 June 1896), 35172 (10 July 1896), 39418, (19 August 1902), and 35169 (26 August 1902) with worn juvenile wing and tail feathers and gorget areas varying from 70 to 95% replaced with iridescent feathers (P. Pyle pers comm.). Some Formative males may approach Definitive appearance by May–July (in North American populations) but gorgeted areas typically duller and/or mottled gray, the result of incomplete replacement and smaller iridescent feathers (see 12), and black

areas of underparts mixed with browner juvenile feathers. Juvenile wing feathers become paler brown and more worn by spring than in Definitive Basic Plumage; juvenile rectrices thinner than basic rectrices, the whitish tips sometimes lost with wear but scalloped tip allows identification of worn juvenile rectrices in May–July.

Female. Similar to Juvenile female but upperparts increasing replaced by brighter green or bronze-green (less olive) feathers, without grayish fringes. Molt limits in upeprwing coverts and wear patterns to wing and tail feathers as described for Formative male.

Definitive Basic Plumage

Present primarily September–August.

Male. Crown rich metallic violet or royal purple, the forehead (at least anteriorly) blackish, usually glossed with green or bluish green; hindneck, sides of occiput, and auricular region velvety black when viewed with bill toward observer and metallic bronze, bronze-green, or golden green with bill away from observer; small white postocular spot or streak (sometimes also a whitish rictal streak) present; remainder of upperparts metallic bronze, bronze-green, or golden green; rectrices bronze-green or golden green with dusky to sooty wash medially across both webs, the outer rectrices sometimes with narrow whitish to pale grayish tips when fresh (but less so than in juvenile male feathers); remiges dark brownish slate or dusky, faintly glossed with purple or purplish bronze. Chin and throat with brilliant metallic emerald green gorget (more yellowish when viewed with bill towards observer, more bluish when viewed from above) extending laterally to sides of nape; upper breast velvety black when viewed with bill toward observer or bronze to bronze-green when viewed with tail toward observer, passing into dusky bronze or bronze-green on lower breast and grayish brown or sooty grayish on abdomen and flanks; femoral and anal tufts white; undertail coverts light brownish gray (sometimes glossed with bronze or bronze-green) margined more or less distinctly with whitish.

Female. Upperparts including central four rectrices metallic bronze to bronze-green, the crown duller (sometimes dull grayish brown anteriorly); outer three rectrices (on each side) with basal half (more or less) bronze-green, blending distally to blackish, and distinctly tipped white, the tips broadest on outermost rectrix and limited to small tip on third; facial area with white postocular streak or spot and dusky auricular area; remiges as in adult male; underparts brownish gray to buffy grayish, glossed laterally with metallic bronze or bronze-green, the feathers of chin and throat margined dull grayish white, producing squamate appearance; femoral and anal tufts white; undertail coverts brownish gray (sometimes glossed bronze-green) margined pale brownish gray or dull whitish.

Molts

General

Molt and plumage terminology follows Humphrey and Parkes (10), as modified by Howell (11) and Howell et al. (13). Rivoli's Hummingbird exhibits a Complex Basic Strategy (*cf.* 11, 14),

including a Preformative Molt, a complete Definitive Prebasic Molt, and possibly an Auxiliary Preformative (First Presupplemental) Molt following fledging, but no Prealternate Molts (3, 5, 8, 6). Preformative Molt traditionally reported as complete, but specimen re-examination by P. Pyle indicates that it is partial rather than complete (see Formative Plumage), as is the case in other large and primitive tropical hummingbirds (15, 16, 17), and that no auxiliary preformative molt occurs. Although prealternate molts have recently been documented in Ruby-throated and Rufous hummingbirds (18, 19), these molts are more frequent and/or more extensive in long-distance migrants than in residents and short-distance migrants (8, 20, 14), and it thus seems probable that Rivoli's Hummingbird lacks a Prealternate Molt.

Prejuvenile (First Prebasic) Molt

Complete, primarily May–July in North America. No information on timing or sequence of pennaceous feather irruption and development. Presumably completed or near completed during nestling period of ca. 25 days (see Breeding: Young Birds).

Preformative Molt

Considered Auxiliary Preformative (First Presupplemental) Molt, in part, by Pyle (8). Partial, apparently very protracted, commencing in some birds as early as June after fledging and possibly concluding in some as late as April or May of second calendar year (Figure 2pertaining to North American breeding populations); commences on summer grounds and completes on winter or summer grounds. Variably includes some to most body feathers, with gorget feathers in males partially or mostly replaced by spring, but few or no upperwing coverts and no primaries, secondaries or rectrices. Males molting head feathers regularly seen in late May and juvenile rectrices retained until second summer in the Huachuca Mountains of southeastern Arizona (S. Williamson and T. Wood, personal communication) and in mid June in the Chiricahua Mountains of southeastern Arizona (E. Sandlin, personal communication; DRP). Sequence appears to begin with throat gorget feathers, with those of head replaced later during molting period.

Definitive Prebasic Molt

Complete, primarily August–February (Figure 2), commencing on summer grounds (possibly occurring during migration [21], though confirmation is needed), and completing on overwintering grounds. Timing appears earlier in migrant North American populations than in populations of southern Mexico and Central America (3). Molt begins with primaries, followed by secondaries and rectrices when primary molt about half completed (21), as in other hummingbirds (22, 12). Primaries likely replaced distally (p1 outward) except outermost (p10) replaced before penultimate (p9) feather, as is typical of other hummingbirds (21, 22, 8). This variant replacement sequence results in stronger (new) outermost primary (p10) when longest primary (p9) is being replaced, which may maximize flight capabilities in hummingbirds, which rely on precision flight (14). Secondaries likely replaced from 2 foci, outermost (s1) inward and innermost (s6) outward, as in other hummingbirds (21, 22, 12, 17). Report that molt begins with the central primaries and progresses in both directions, and that replacement of secondaries proceeds proximally (from s1 to s6) in simple continuation of the primary molt (21) is unlikely,

and would represent novel remigial sequence in birds. Sequence of rectrix replacement appears to parallel that of most other hummingbirds (22, 12), commencing with the central rectrix (r1) and generally proceeding laterally to the outermost feather (r5) on both sides of tail (21).

Replacement of body feathers reported to occur during latter portions of flight-feather molt (21) but more likely occurs gradually throughout period of flight-feather replacement, perhaps peaking when secondaries and rectrices molting (22). Modified ornamental gorget feathers of males replaced rapidly toward completion of molt (21, 23), as in other hummingbirds (22, 12). Other hummingbirds can retain rectrices or other feathers during incomplete Second and later Definitive Prebasic Molts (12), and this might be expected in Rivoli's Hummingbird as well (8).

Bare Parts

Bill

Dull black (4) to black, with lower mandible pinkish basally, more so in younger females (24). In the closely-related Talamanca Hummingbird, the bill is softer in juveniles, with distolateral corrugations on base, extending to 75% of base of bill for a 5-month period post fledging (F. G. Stiles, personal communication; *cf.* 25), gradually diminishing (through wear and bill-hardening process) to < 10% of bill by December–March of first year; presence of corrugations useful for ageing (26, 8; *cf.* 27). Adults with smooth bill bases or corrugations or extending < 10% at base (8).

Iris

Dark brown (4) or blackish brown (24).

Legs and Feet

Dusky (4) or blackish brown, paler in juvenile (24).

Linear Measurements

See Appendix 1.

Mass

Males

Capture mass of 47 *E. fulgens* males, June and July in Chiricahua Mountains, Arizona, was reported as 7.90 g ± 0.49 SD (range 6.81–9.55) (DRP). Mass (energy storage) does not change substantially with time of day. Few mass data are available on birds at dusk, so it is unknown if they experience a mass peak (due to intense feeding) prior to roosting. Mass of six captive birds that fasted for 1 hour was 7.52 g ± 0.30 SD (range 6.98–7.89), only 4.8% lower than average

capture mass (DRP). Prior to roosting, these birds consumed 0.68 g ± 0.37 SD (range 0.20–1.05) of food, increasing their mass by about 9%, most of which was water. It is unlikely that this is sufficient to support nighttime metabolism totally and may explain why birds appear to use torpor at night routinely (see Diet and Foraging: Metabolism and Temperature Regulation).

Females

Capture mass of 14 *E. fulgens* females in June and July in the Chiricahua Mountains, Arizona, was 7.34 g ± 0.35 SD (range 6.74–8.10) (DRP). No data available on diurnal mass change is available for females.

Systematics

Geographic Variation

Bill length may increase clinally, if only slightly, from northern Mexico (and the southwestern United States) south to Nicaragua. Ventral coloration varies, perhaps clinally, along this same axis, being blackest in the north and palest (but still a blackish gray) in the south.

Subspecies

With the split of birds from southern Central America (see Related Species), there are no subspecies, although note that *Ornismya rivolii* Lesson, 1829; *Trochilus papantzin* de la Llave, 1833; *E. f. viridiceps* (Boucard, 1878); and *E. f. aureoviridis* van Rossem, 1939, are junior synonyms of *Eugenes fulgens* (Swainson, 1827).

Related Species

Within the distinctive hummingbird family (Trochilidae), the monotypic genus *Eugenes* sits in the "mountain-gem" radiation, tribe Lampornithini (28, 29), a radiation that also includes the genera *Lampornis* (mountain-gems), *Heliomaster* (starthroats), and *Panterpe* (*P. insignis*, the Fiery-throated Hummingbird of Costa Rica and Panama). Zimmer (30) suggested that *Eugenes* be merged with the speciose, predominantly South American genus *Heliodoxa* on the basis of the "long forward extension of the frontal feathering, covering the nasal operculum, and an equal extension of the chin plumage," and Powers (31) stated the "genus [is] sometimes merged into *Heliodoxa*." However, Wetmore (32) pointed out "that in *Heliodoxa leadbeateri*, the type species of *Heliodoxa*, the operculum is covered with feathers while in *Eugenes fulgens* it is bare" and suggested that until more information is available *Eugenes* should remain separate. Wetmore's assessment has been supported by molecular phylogenetics (28, 29): *Heliodoxa* is in a separate radiation, the "brilliants" (tribe Coeligenini).

On the basis of the larger mean body size, slight differences in plumage color (e.g., the gorget is bluer and the crissum is grayer), and, perhaps most of all, allopatric distribution, various

authorities argued that birds in Costa Rica and Panama were specifically distinct (33, 31, 34), but the American Ornithological Society did not "officially" treat it as a species, *E. spectabilis*, the Talamanca Hummingbird, until recently (2). *E. fulgens* and *E. spectabilis* are sister species.

Four instances of natural hybridization involving *E. fulgens* have been recorded, only one of them involving a species in the same tribe: *Lampornis clemenciae*, the Blue-throated Hummingbird (7). The other hybrids were more surprising, even given the high rates of inbreeding among species of hummingbirds. A male specimen from southeastern Arizona is a hybrid with *Cynanthus latirostris*, the Broad-billed Hummingbird (35), a putative cross with *Amazilia violiceps*, the Violet-crowned Hummingbird, was determined from a photograph (7), and putative crosses with *A. beryllina*, the Berylline Hummingbird, have been reported in southeastern Arizona (7).

Distribution, Migration, and Habitat

Distribution in the Americas

Breeding Range

Figure 1. Breeds from the extreme southwestern United States south through much of Mexico and Central America. In the U.S., breeds in mountains of southeastern Arizona (including Santa Rita, Santa Catalina, Huachuca, Chiricahua, and Pinaleno mountains (36), extreme southwestern New Mexico, including the San Luis Mountains (37), and possibly in the highlands of northern New Mexico (38). However, current breeding status in New Mexico is unclear; e.g., not recorded during the New Mexico Breeding Bird Atlas (2000–2011).

Also an uncommon summer resident, probably breeding, in the Chisos Mountains of western Texas (39, 40). Oberholser (5) reported the collecting of a female during the summer of 1972 at McKittrick Canyon, Culberson County, Texas with a well-developed brood patch and ovaries.

In Mexico, breeding status is largely assumed based on summer residence and breeding condition of collected specimens. Believed to occur in highlands of most mainland states from the U.S. border south to Chiapas (41, 9). Specific records (only mountain ranges or nearest city given) include: Sonora (Sierra Madre Occidental and adjacent ranges, San Luis Mountains; 42, 43, 37); Chihuahua (Sierra Madre Occidental and adjacent ranges; 43); Coahuila (Sierra del Carmen [44]; Sierra Guadalupe [45]); Nuevo León, Jalisco (Volcán de Nieve and Sierra de Autlán; 46); Colima (Volcán de Colima; 47); Michoacán (Valaroso, Dos Aguas, La Nieve, Puerto Verde; 48); Queretaro (Maguey Verde; 48); Distrito Federal (Ciudad Universitaria, Contreras Primer Dinamo; 49, 48); Tlaxcala (Campamento IMSS Malintze; 48); Guerrero (Sierra Madre del Sur; 48); Morelos (northern Cuernavaca; 48); Puebla (Zacatlán; 48); Veracruz (southern Veracruz, Sierra Madre Oriental; 48), Oaxaca (Sierra Madre de Chiapas, Sierra Aloapaneca, Sierra de Cuatro Venados, Sierra de Oaxaca; 50, 51); and Chiapas (San Cristóbal de las Casas; 48).

In Central America, Guatemala (highlands; 52), El Salvador (Los Esesmiles and Volcán de Santa Ana; 24), and Honduras (Cordillera Central and Cordillera Sur; 53). Slud (54) states that the species "is not known from the northwestern divide," creating a significant gap between the Nicaraguan populations of Rivoli's Hummingbird and the northernmost populations of the formerly conspecific Talamanca Hummingbird.

Vagrant records in the U.S. during breeding season include Arizona (e.g., White Mountains, South Rim Grand Canyon, Flagstaff, and Prescott; 55), western and north-central Colorado (49 records from at least 15 counties; one nest recorded in Boulder County in July 1965; 56, 57), eastern Kansas (Boicourt and Linn counties; 58), south-central Texas (5), and northern Utah (Springdale and Washington counties; 59).

Overwintering Range

Figure 1. Birds resident throughout breeding range except in U.S. (55), northern Mexico (Sonora, Chihuahua, Coahuila, and Nuevo León; 42, 9), and parts of central Mexico (Distrito Federal and Mexico City area; 60). Recorded regularly in small numbers in the southwestern U.S., primarily in Arizona, where the species has repeatedly overwintered in lower mountain canyons, primarily at feeders (55).

Distribution Outside the Americas

No records.

Nature of Migration

Few data; needs study. Breeding populations in U.S., northern Mexico, and parts of central Mexico are migratory; populations appear to be resident in remainder of range. Dynamics of migration are poorly studied, but individuals that do migrate probably travel a relatively short distance in order to find suitable nesting habitat where food is abundant. Altitudinal migration has been documented for several populations in the southern portion of the range (e.g., Honduras [53]; Guatemala [52]; Volcán de Colima, Mexico [47]).

Timing and Routes of Migration

Most individuals reach the southwestern U.S. in late March or early April (see Figure 2), with earliest observations in Arizona in early March (61). In New Mexico and Texas (Chisos Mountains), first sightings in April (e.g., 37, 39, 5, 38, eBird 2018). Males in U.S. appear to be highly transient; rarely in one place for any length of time. Of > 100 males color-marked in the Chiricahua Mountains between March and July 1995, few were subsequently seen with any regularity (E. Sandlin, personal communication).

Because females begin nesting in April (Figure 2), they are probably less transient than males, but female movements have not been formally studied. There are many extralimital records of birds throughout the western U.S., but Johnsgard (62) suggested that these result from the

dispersal of postbreeding juveniles and adults. Birds typically leave the U.S. in late September or early October, but some linger in Arizona into mid November (63), and records during winter months suggesting existence of resident individuals (e.g., 37, 38, eBird 2018).

Migratory Behavior

No information.

Control and Physiology of Migration

No information.

Habitat in Breeding Range

United States and Northern Mexico

Locally common in mixed Sonoran and upper transition zones (63), ranging in elevation from 1,500 to at least 2,740 m (43, 45, 63, 41, 9, 61). In Colorado, few sightings, but all from > 2,500 m (56). Presence of species at higher altitudes is probably explained by availability of suitable flowers and insects during late spring and summer (64). Found in canyon bottoms along streams, but does not appear to be as closely associated with riparian habitats as Blue-throated Hummingbird, which is often sympatric (43, DRP).

Generally common in mixed oak, pine (Ponderosa Pine [*Pinus ponderosa*], Chihuahua Pine [*P. leiophylla*], Mexican Pinyon [*P. cembroides*]) and juniper (Alligator Juniper [*Juniperus deppeana*]) forest (e.g., 43, 39, 65, 66). Also Arizona Alder (*Alnus oblongifolia*), Arizona Cypress (*Cupressus arizonica*), Arizona Sycamore (*Platanus wrightii*), Douglas-fir (*Pseudotsuga menziesii*), and Arizona Walnut (*Juglans major*) (67, 68, 69, 66; P. Scott, personal communication, DRP). Species often feeds in more open and otherwise disturbed areas where appropriate flowers are most abundant.

In Arizona, breeding atlas records mostly at 1,600–2,700 m, in Madrean pine–oak forests and cooler mixed-conifer associations (uneven-aged stands of Ponderosa Pine, Douglas-fir, Colorado White Fir [*Abies concolor*], and Quaking Aspen [*Populus tremuloides*]) at higher elevations or farther north; individuals known to descend to lower canyon feeding stations, dominated by evergreen oaks and sycamores, but nests almost always at higher elevations in canyons and conifer-dominated slopes (61).

Southern Mexico and Central America

As in more northerly populations, typically found at elevations between 1,500 and 2,500 m. Although nonmigratory in this region, observed to move to lower elevations during colder months of the year; e.g., in Guatemala descends below 900 m from December to February (52). Typical habitat ranges from upper arid tropical zone with seasonal rainfall (e.g., much of southern Mexico and lower elevations in Central America; 24, 50, 47) to more humid cloud

forests at upper end of the elevational range of this species (46, 47, 51). In regions where rainfall is seasonal, rainy season is fall or winter. For example, rainy season in upper arid tropical zone of El Salvador typically lasts from May through November (24). Throughout this portion of its range, Rivoli's Hummingbird is most common in arid pine–oak or oak forests (24, 43, 46, 47) and in humid pine–oak forest (47, 51), although other tree types are occasionally important (e.g., 50, 26). This species typically frequents forest edges or breaks, park-like pastures, and thinned woodlands where preferred flowers grow in abundance (54, 26).

Habitat in Migration

No information.

Habitat in the Overwintering Range

No data for migratory populations in U.S. and northern Mexico. In southern Mexico and Central America winter range overlaps with breeding range.

Historical Changes to the Distribution

None reported.

Fossil History

No information.

Diet and Foraging

Feeding

Main Foods Taken

Like other hummingbirds, consumes floral nectar from several plant species and catches small insects in the air or gleans them from foliage. Nectars preferred are like those preferred by other hummingbirds—containing primarily sucrose and low quantities of other substances such as amino acids (70, 71, 72). Individual Rivoli's Hummingbirds have shown the ability to discriminate among nectars of different sugar concentrations and may use color as a cue to target flowers with higher concentration (70, 73). Hainsworth and Wolf (70) suggested best discrimination occurred at concentrations below about 0.7M although Sandlin (73, 74) showed clear preference for 0.86 over 0.43M sucrose. When nectar sugar concentration is low (~5%), Rivoli's Hummingbirds will switch from a sucrose preference to a glucose preference (75). Nectar-extraction rate appears related to corolla length, with highest extraction rates measured for corollas < 30 mm (55–70 ml/s) (70). A lower extraction rate was measured from artificial feeders (35.7 µl/s) (73).

Diet

Nectar

United States. Surprisingly little is known about the flowers preferred by this species, but some flower species that have been identified or are suspected to be visited include: century plant (*Agave* spp.), Red Columbine (*Aquilegia triternata*), Bouvardia (*Bouvardia ternifolia*), indian paintbrush (*Castilleja* spp.), Mojave Mound Cactus (*Echinocereus polyacanthus*), Beardlip Penstemon (*Penstemon barbatus*), Jacob's Ladder (*Polemonium pauciflorum*), Lemmon's Sage (*Salvia lemmonii*), and Indian Pink (*Silene laciniata*) (66, 64, 65; B. Hoyer, personal communication).

In southeastern Arizona visits Giant Trumpet (*Macromeria viridiflora*; Boraginaceae), which grows in mountainous areas between 1,500–3,000 m (76). Flowers of *M. viridiflora* in southeastern Arizona (where they are used by *E. fulgens*) are larger than in northern U.S. populations, suggesting pollinator-mediated selection (76).

Mexico. In Volcán de Colima, southern Mexico, flowering plants available to Rivoli's Hummingbird between 1,500 and 2,500 m in the arid pine–oak forest include: thistle (*Cirsium* spp.), Fuchsia (*Fuchsia parviflora*), Lion's-ear (*Leonotis nepetaefolia*), Vervain (*Lippia umbellata*), Bellflower (*Lobelia laxiflora*), Rose of Sharon (*Malvaviscus arboreus*), bean (*Phaseolus formosus*), and sage (*Salvia mexicana*). Rivoli's Hummingbird is rarest during summer in this region, but more common when thistle and bellflower come into bloom. Above 2,500 m, flowers include: Butterfly Bush (*Buddleia cordata*), Nightblooming Jessamine (*Cestrum terminale*), thistle (*Cirsium* spp.), Beard-tongue (*Penstemon roseus*), current (*Ribes ciliatum*), and Snowberry (*Symphoricarpos microphyllus*). Rivoli's Hummingbird is permanent resident in this habitat where it forages as a trapliner primarily on *Cirsium* thistles, although it frequently feeds on beard-tongue if present (47). Des Granges (47) describes Rivoli's Hummingbird as a specialist on long-corolla flowers.

In Parque Nacional La Malinche, Tlaxcala (2,900 m elevation), where vegetation is a mosaic of pine-oak forest, pasture, and second-growth vegetation, individuals regularly visit Bouvardia (*B. ternifolia*) between May-August (77).

In areas surrounding Mexico City and Distrito Federal, Rivoli's Hummingbird commonly defends Century Plant (*Agave salmiana*); this plant forms many flowers, each of which produces about 3.5 ml/12 h of nectar containing 12–13% sugar (49). Although sugar concentration of this plant's nectar is relatively low for a hummingbird flower, the tightly clumped arrangement of the flowers probably increases foraging efficiency (49). In Hildago, Mexico (~92 km north of Mexico City), Rivoli's Hummingbirds feed on “honeydew” produced by scale insects in the genus Strigmacoccus (Margarodidae) whose secretions are ~35–45% sugar (78). In Tlaxcala, Mexico (~62 km southeast of Mexico City), Rivoli's Hummingbirds feed from and pollinate the mistletoe *Psittacanthus calyculatus*(Loranthaceae) that flowers from April–October with each flower producing 2.3 µL of nectar containing 22% sucrose (79). In areas around Tlaxcala Rivoli's Hummingbirds also feed on Bouvardia, indian paintbrush (*C. scorzonerifolia* and *C.*

tenuiflora), sage (*S. elegans* and *S. mocinoi*), penstemon (*P. getianoides* and *P. roseus*), and common heal-all (Prunella vulgaris) (80).

On Cerro San Felipe, Oaxaca, flowers commonly used by Rivoli's Hummingbird from June to September are beard-tongue (*Penstemon kunthii*) and iris (*Rigidella orthantha*). The iris occurs in dense scattered stands near streams and open areas and is an important food source in May, less so after mid June. Beard-tongues' peak blossoming period is early August through October; like the iris, it is confined to open areas. Used by Rivoli's Hummingbirds as well as other hummingbirds during this period: indian paint-brush (*Castilleja* spp.), thistle (*Cirsium mexicanum*), Cuphea (*Cuphea jorullensis*), *Lamourouxia viscosus*, lobelia (*Lobelia laxiflora*), *Macromeria doscolor*, sage (*Salvia stolonifera*), *Satejura mexicana*, and Scarlet Betony (*Stachys coccinea*). These species, however, were simply occasional food sources and not important to territorial dynamics (50).

Near Xalapa City, Veracruz, *E. fulgens* is an infrequent visitor of *Palicourea padifolia*, which grows at mid-level elevations in cloud forests (81).

Insects

Rivoli's Hummingbirds may be more insectivorous than other North American hummingbirds (e.g., 43, 82). Marshall (43) suggests that Rivoli's Hummingbirds can inhabit pine-oak woodlands away from riparian areas because the species “can dispense with both moist habitat and flowers.” In the Chiricahua Mountains of southeastern Arizona, birds placed in aviaries survived > 2 h without drinking nectar while actively catching insects (E. Sandlin, personal communication; DRP). Behavior of free-living males is consistent with high-arthropod consumption (83).

Crops of captives often have full and diverse arthropod loads (84). Of 12 wild birds collected for stomach analysis, all contained arthropods (85, 43, 86); three individuals examined by Cottam and Knappen (85) had consumed a variety of insects and spiders; 6 males examined by Powers et al. (83) consumed 2 classes and 4 orders of arthropods.

Rivoli's Hummingbird lives in many areas that have a distinct dry season, where free-standing nectar can be in short supply. Nevertheless, Powers et al. (83) found no morphological specialization that suggested adaptation for increased arthropod foraging relative to other hummingbirds. The maintenance nitrogen requirement of Rivoli's Hummingbirds is 4.03 mg N/d (only 23.6% the predicted value), suggesting their protein requirement is low as has been shown with other hummingbird species (87).

Food Selection and Storage

Laboratory studies suggest that Rivoli's Hummingbird makes food choices based on sugar concentration, and secondarily on nectar extraction efficiency (70). In the Chiricahua Mountains, Arizona, Rivoli's Hummingbird may select sugar-poor food source when Blue-throated Hummingbird territorial activity is high (88).

Nectar is stored only in the crop. Crop volume ranges from 0.9–1.1 ml (mass 7–10 g) (89).

Nutrition and Energetics

Nectars used by hummingbirds are generally simple, containing primarily carbohydrate (primarily sucrose) and water. Small amounts of amino acids and electrolytes may be present but are generally not sufficient to meet all nutritional needs (72, 90).

No direct measurement of daily energy expenditure. Using time budgets, Wolf et al. (91) estimated total daily energy expenditure of Talamanca Hummingbirds in Costa Rica to be about 64 kJ/d when feeding on *Cirsium* thistles (45 kJ/d when using torpor at night) and about 65 kJ/d when feeding on *Centropogon* (46 kJ/d when using torpor). These estimates are based on numerous assumptions and are probably low. For comparison, field metabolic rate of the similarly sized Blue-throated Hummingbird in the Chiricahua Mountains of southeastern Arizona determined by doubly labeled water is 82 kJ/d (92), 74% higher than the time-budget estimate for Rivoli's Hummingbird.

Hainsworth et al. (93) measured feeding rate of Rivoli's Hummingbird from the Chiricahua Mountains (sex not reported, but probably males) in the laboratory and determined that they consumed 11.8 ± 2.8 meals/h (mean ± 95% confidence limit) of 17% sucrose, with a meal size of 190 ± 19.0 µl (< 20% of predicted crop volume [1.05 ml]) (89). No measurement of feeding frequency has been made on free-living Rivoli's Hummingbirds. Blue-throated Hummingbirds in the Chiricahua Mountains consumed about 8 meals/hour (92), 32% fewer than Rivoli's Hummingbirds in the laboratory. If feeding frequency and meal size are representative of free-living Rivoli's Hummingbirds in the Chiricahua Mountains, then the foraging pattern that might be expected for this traplining population is frequent small meals that reduce flight costs (94). Small, rapidly metabolized meals are consistent with lower respiratory quotient in this species (0.767 ± 0.012) compared to sympatric Blue-throated Hummingbird (0.828 ± 0.068) and Black-chinned Hummingbird (0.851 ± 0.194) (83).

Metabolism and Temperature Regulation

Rivoli's Hummingbird maintains a constant body temperature of about 40°C (95). Basal metabolic rate (BMR) of Rivoli's Hummingbird in the Chiricahua Mountains of southeastern Arizona is 0.054 kJ $g^{-1}h^{-1}$, within the zone of thermal neutrality (32–34°C) (96), which is 10.2% higher than that predicted by Aschoff and Pohl (97) for a nonpasserine bird of the same size. From 30° to 5°C, metabolic rate increases linearly to maintain constant body temperature (96). The slope of this line is the rate of heat loss (thermal conductance) and is 6.03 kJ $g^{-1}h^{-1}°C^{-1}$for birds in the Chiricahua Mountains (96). This high rate of heat loss is consistent with the fact that small animals must work harder (i.e., have a higher rate of heat production) to maintain homeothermy. Hovering metabolic rate of Rivoli's Hummingbirds in the Chiricahua Mountains of southeastern Arizona is 0.62 kJ $g^{-1}h^{-1}$, which is 11.5 x BMR (D. Powers, unpublished data).

Small size also effects evaporative water loss (EWL), an important mechanism for dissipating heat. EWL in Rivoli's Hummingbirds ranges from 6.7 to 12.5 mg H_2O $g^{-1}h^{-1}$ between 15 and

25°C, respectively, in relatively dry air (96). At 25°C, EWL is 17% lower than that measured for Anna's Hummingbird (*Calypte anna*; about 4.5 g, the highest value measured for any vertebrate) under similar conditions (98). During hovering, respiratory evaporative water loss (REWL) in Rivoli's Hummingbirds increases with operative temperature (Te) (males: log REWL [mg/min] = $1.600Te^{-1.517}$; females: log REWL = $1.486Te^{-1.495}$ (99).

The high metabolic requirement of Rivoli's Hummingbird is consistent with the fact that it has one of the highest recorded heart rates of any vertebrate (range 420–1,200 beats/min) (96). This does not differ substantially from that of other hummingbirds, even those of smaller size, indicating that the heart of a Rivoli's Hummingbird may be working at maximum capacity for its cardiac system.

Like most hummingbirds studied, Rivoli's Hummingbird has the ability to enter torpor at night to reducing nighttime energy expenditure but will avoid torpor when energy intake is high (100). Wolf and Hainsworth (95) observed individuals regularly entering torpor below 30°C. In experiments where birds from the Chiricahua Mountains were exposed to natural nighttime temperatures, birds entered torpor about half the time; torpor appears to be used when total body fat falls below 4% (100). It is unclear from these experiments if time or temperature influence torpor use.

Torpor metabolism of Rivoli's Hummingbird in the Chiricahua Mountains ranges from 0.1 ml $O_2g^{-1}h^{-1}$at 14.9°C to 1.18 ml $O_2g^{-1}h^{-1}$ at 26.9°C (96). These values support Wolf and Hainsworth's (95) view that Rivoli's Hummingbird enters torpor even at relatively warm temperatures (< 30°C).

Steady-state oxygen consumption of torpid birds decreases with temperature in an exponential fashion. When ambient temperature drops below 14°C for birds in the Chiricahua Mountains (101), oxygen consumption increases, presumably to defend some minimum body temperature.

Drinking, Pellet-Casting, and Defecation

Free-living hummingbirds consume, on average, 1.6–1.7 times their body weight in fluids via nectar each day (102, 92), but captive Rivoli's Hummingbirds have been shown to consume as much as ~3.5 times their body weight in fluids (87). This more than meets the birds' physiological needs, thus eliminating the requirement of drinking free water. If its excretory system has the same characteristics found in several smaller species, then it produces cloacal fluids that are more dilute than blood plasma (103). Total nitrogen loss in Rivoli's Hummingbirds is 1.98 mg N/d, most of which (84.6%) is excreted as urates (87).

Sounds and Vocal Behavior

Vocalizations

Vocal Array

Chip. See Figure 3A. Recorded only for adult males. Heard while bird is perching or in flight. Component parts range in frequency from about 4–8 kHz. Interval between chips is highly variable, ranging from 0.1 to 1.5 s. Shortest intervals, 0.1–0.2 s, occur periodically during the call when a pair of chips are given in rapid succession. These calls are common in *E. fulgens.*

Aggressive Chatter. See Figure 3B. Complex vocalization. Sounds like series of chip notes run together in rapid succession when bird is alarmed. Common vocalization given during aggressive encounters (26; P. Ficken, personal communication).

Contact-spacing Note. "Given while perched or flying (especially while foraging). A rolling, rather guttural *nrrt* or *drrk* " (F. G. Stiles, personal communication). This description is based on observations of *E. spectabilis*; it has not been described for *E. fulgens*.

Whisper Song. See Figure 3C. This description is based on observations of *E. spectabilis*; it has not been described for *E. fulgens*. Heard only during the breeding season. Stiles and Skutch (26) note that "Males have a soft, low-pitched song of burbling, scratchy notes, given in courtship interactions or while perched on territory." May also be used by males during aggressive interactions, when perched (F. G. Stiles, personal communication). Song of *E. fulgens* may be slightly higher in pitch (F. G. Stiles, personal communication).

Nonvocal Sounds

None known. During a 3-year study in Oaxaca, Mexico, no bird exhibited any sort of display-associated sound other than the rapid cheeping (Aggressive Chatter) described above (50).

Behavior

Locomotion

Flight

The only means of locomotion is flight; feet and legs are incapable of walking or hopping, and only used for perching. Hovering flight is used for nectar foraging; brief forays involving both hovering and forward flight are used for catching arthropods, and forward flight (often rapid) is used for transport and aggression. Wingbeat frequency during hovering flight is 22 beats/s (96). Cost of flight has not been measured, but probably 10–11 times resting metabolic rate (e.g., 104).

Measured values for wing disc loading have ranged from 0.038 to 0.055 g/cm^2 (47, 93; E. Sandlin, personal communication). These values are high compared to those measured for other hummingbirds, and are in the range of values exhibited by strongly territorial species (105). Rivoli's Hummingbird is not consistently territorial (see Spacing and Agonistic Behavior), so the reason for high wing disc loading is unclear. Although to date no relationship between flight or hovering costs and mass or wing disc loading has been identified, it has been suggested that higher wing disc loading should decrease the energetic efficiency of flight (e.g., 106, 105).

Self-Maintenance

Preening

Similar to other hummingbirds. Scratches head and heck with feet, grooms feathers with bill. Fluffs and shakes when wet. Cleans bill by wiping it on a branch.

Hypothermic Torpor

Use of hypothermic torpor at night (see Diet and Foraging: Metabolism and Temperature Regulation) in the Chiricahua Mountains, southeastern Arizona, appears variable and is likely related to daily food intake (100). Even though Rivoli's Hummingbird seems to thrive in most in environments where energy availability is high (see Spacing), energy expenditure is probably high enough that torpor is needed frequently.

Daily Time Budget

Not described for Rivoli's Hummingbird. Complete time budgets measured only for the closely-related Talamanca Hummingbird in Cerro de la Muerte, Costa Rica (91). Males feeding at *Cirsium* thistles budgeted their time as follows: perch 86.4%, forage 7.3%, chase 2.1%, flight 0.8%, and out-of-sight 3.3%. Males feeding at *Centropogon*: perch 85.1%, forage 9.7%, chase 1.6%, flight 0.2%, and out-of-sight 3.4% (91). These data suggest that males perch for longer periods and fly less than other hummingbirds with which they overlap (e.g., Fiery-throated Hummingbird perches 43–70% of the time; [91]).

Agonistic Behavior

Males are highly territorial in some areas, yet nonterritorial in others. Territorial behavior has been observed in Oaxaca, Mexico, where males were codominant with the Blue-throated Hummingbird (50). In this system, dominance is a function of body size; male Rivoli's Hummingbird is able to intrude into territories of smaller species are unmolested while excluding other hummingbirds efficiently from their own territories. Male Rivoli's Hummingbird was just as efficient as Blue-throated Hummingbird, one of the more aggressive species studied, in excluding intruders. Female Rivoli's Hummingbird is occasionally observed to hold territories, but these were usually temporary and smaller than those defended by males.

Near Mexico City and Distrito Federal, males actively defend flowers of *Agave salmiana* (49). Around Mexico City, males repel essentially all hummingbird intrusions, although perching birds that compete for nectar are generally ignored. Intrusion pressure is generally low, as only 27 intrusions observed. Intrusions are somewhat more successful near Presidio Sur, although most (183 of 203 intrusions) are still repelled by territorial males; success is apparently due to denser vegetation and increased intruder pressure, causing aggression to be more intensified. Females never observed to be territorial in this system.

In Volcán de Colima, Mexico, and southeastern Arizona, Rivoli's Hummingbird are not known to be territorial. Des Granges (47) described birds in Volcán de Colima as being “trapliners” (cycle among widely scattered flowers to feed). In southeastern Arizona, individuals do not seem to be tied to any nectar source and appear to range widely, behaving much like a trapliner (Sandlin 2000, DRP). Pimm (69) describes the role of Arizona birds as “one of being unpredictable.” In general, ability of male Rivoli's Hummingbird to be territorial appears to depend on resources available.

Spacing

Not surprisingly, density of males is highest when flower abundance is greatest. In Oaxaca, Mexico (50), males were most territorial during peak *Penstemon* blooms (after 15 July). During this time, territory sizes averaged 722.6 m^2 ± 265.4 SD and occurred where flowers were densely packed; territories were maintained for as long as 12 wk. Males never attempted to defend smaller, more scattered stands of *Penstemon*, indicating some minimum nectar requirement. These examples suggest that territoriality is energetically expensive. Generally, birds seem to require relatively high volumes of nectar that can be found efficiently.

Individuals studied in Volcán de Colima, Mexico, and southeastern Arizona apparently function as trapliners (see above). In southeastern Arizona, birds are abundant but highly transient. Sandlin (74) color-marked 123 individuals during spring and summer 1995 at the Southwestern Research Station in the Chiricahua Mountains. However, no more than a few individuals were ever seen in the area at one time, even though the station has a long history of maintaining feeders. Individuals that were marked appeared at intervals separated by weeks at a time, probably because Blue-throated Hummingbirds forced them into a subordinate role, and because of the absence of preferred dense flower patches in open areas.

Sexual Behavior

Essentially unstudied. Presumably a promiscuous mating system like that of most hummingbirds.

Social and Interspecific Behavior

United States

Males typically subordinate to male Blue-throated Hummingbirds (107, 69, 88, 73, 74, 100) which can result in their need to use poor-quality food sources (74). Throughout the breeding season, male Rivoli's Hummingbirds co-occur with Black-chinned Hummingbird (*Archilocus alexandri*) and Broad-tailed Hummingbird (*Selasphorus platycercus*), but rarely engage in agonistic behavior or interfere with feeding behavior (88, 100). During late June and July, Calliope Hummingbird (*Stellula calliope*), Rufous Hummingbird (*Selasphorus rufus*), and Violet-crowned Hummingbird (*Amazilia violiceps*) invade portions of the Rivoli's Hummingbird range and appear to cause increased dispersal. However, no agonistic behavior has been observed. Berylline Hummingbird and White-eared Hummingbird (*Hylocharis leucotis*)

regularly co-occur with Rivoli's Hummingbirds in very small numbers. No information available on interactions.

Mexico

Male Rivoli's Hummingbird is clearly dominant over Amethyst-throated Hummingbird (*Lampornis amethystinus*), Berylline Hummingbird, Bumblebee Hummingbird (*Atthis heloisa*), and Allen's Hummingbird (*Selasphorus sasin*) (Oaxaca [50]; near Mexico City [49]; Volcán de Colima [47]). Males are moderately dominant (occasionally lose aggressive interactions) over Broad-tailed Hummingbird, Rufous Hummingbird, Violet-crowned Hummingbird, Mexican Violetear (*Colibri thalassinus*), and White-eared Hummingbird (Volcán de Colima [47]; near Mexico City [49]). Des Granges (47) suggests that many of the above interactions vary seasonally because of changes in niche overlap.

The only species to which Rivoli's Hummingbird is clearly subordinate is the Blue-throated Hummingbird in Oaxaca (50). Rivoli's Hummingbirds did displace Blue-throated Hummingbirds during one year of Lyon's (50) study, but Lyon suggested that the displacement was due to an unusually high number of male Rivoli's Hummingbirds in the area which made defending territories for Blue-throated Hummingbirds unprofitable. Male Rivoli's Hummingbirds were able to hold territories at *A. salmiana* flowers, but Blue-throated Hummingbird did appear to be the more aggressive species, successfully intruding on several occasions near Mexico City (49).

Predation

No records of depredation on adults. Miller and Gass (108) suggested that depredation is not an important source of mortality for North American temperate-zone hummingbirds. However, reports by Beebe (109) and Stiles (110) suggested that depredation on tropical populations may be significant.

Nestling survival has been little studied except in Rucker Canyon in the western Chiricahua Mountains of southeastern Arizona (66). Of 2 Rivoli's Hummingbird nests located by Baltosser (66), one was abandoned before eggs were laid, and another fledged 2 young; 68% of all hummingbird (primarily Black-chinned Hummingbird) nest mortality in Rucker Canyon resulted from depredation, probably avian predators such as Mexican Jay (*Aphelocoma wollweberi*), Hooded Oriole (*Icterus cucullatus*), and Summer Tanager (*Piranga rubra*), as well as snakes.

Breeding

Phenology

United States

Few data; a secretive nester. Breeding records from May through July (Figure 2). Earliest record is of a female carrying an unshelled egg (large, firm, but not ridged, mass in lower abdomen) on

23 April at Ramsey Canyon in the Huachuca Mountains of southeastern Arizona (S. Williamson and T. Wood, personal communication). Earliest record of eggs and nest is May (67; various collection records). In the Chiricahua and Huachuca mountains, juvenile birds typically do not show up in mist-netting samples until late June, although the earliest recorded capture of a juvenile is 26 May (S. Williamson and T. Wood, personal communication). In Ramsey Canyon, the bulk of juvenile birds are captured from early August through late September, when mist-netting activities cease (S. Williamson and T. Wood, personal communication).

It is not known whether Rivoli's Hummingbird rears multiple broods like other hummingbird species, but there is ample time to do so.

Central America

Rivoli's Hummingbird may breed year-round in El Salvador based on the February collection of a female containing a nearly formed egg, and collection of second female in Juvenile plumage (24). The closely-related Talamanca Hummingbird breeds mainly during winter flowering seasons (26), which starts around November, peaks sometime between January and May, and extends into June or July (F. G. Stiles, personal communication).

Nest Site

United States

Typically above 1,800 m (recorded range 1,700–3,160 m) (43, 111, 88), in or near canyon riparian habitat. Nests are often constructed on horizontal branches or forks of maples (*Acer* spp.) and sycamores, but also in Colorado White Fir, Douglas-fir, Mexican Alder, and Arizona Walnut (67; W. H. Baltosser and P. Scott, personal communications; unpublished data from several museum collections). Nests are generally placed 2–3 m away from the trunk (often overhanging streams) and at least 6 m above ground (recorded range 3–27 m) (67, 112; W. H. Baltosser and P. Scott, personal communications; unpublished data from several collections).

Nest

United States

Typical of nests reported for other hummingbirds. In southeastern Arizona nests are open cup with soft downy feathers and mosses (67; unpublished data from several museum collections). Exterior is liberally covered with lichen (112, 67; P. Scott, personal communication; unpublished data from several collections). Dimensions (cm): external diameter 5.7, internal diameter 2.9–3.8, external depth 3.8–5.1, internal depth 1.9–3.2 (n = 43) (67). One nest in Colorado was composed of parts from seeds and capsules of aspen (*Populus*) and wooly portions of willow (*Salix*) catkins; materials bound together by spider silk (56); outer portion lined with lichen and pieces of bark like nests in Arizona. Dimensions (cm): outer diameter 5.7, inner diameter 3.1, similar to nests collected in Arizona (56). Bent (67) and Reed (112) suggested that the nest most

closely resembles that of Ruby-throated Hummingbird (*Archilochus colubris*), only larger and broader.

Eggs

Clutch of 2 white, smooth-surfaced, oval eggs. Two unpublished observations by F. Willard (1897 and 1913) suggested that laying may be asynchronous with an interval between eggs of one to “several” days. Mean dimensions: 15.4 × 10.0 mm (extremes 16.5 × 10.4 mm; 15.3 × 11.4 mm; 14.0 × 10.0 mm; 15.1 × 9.4 mm) (*n* = 43; [67]); 16.5 × 10.2 mm (sample size unknown; [112]); and 15.44 mm (range 14.70–17.14) × 9.82 mm (range 9.05–10.33, *n* = 13) (Western Foundation of Vertebrate Zoology [WFVZ]).

Eggshell mass 0.043 g (range 0.032–0.048, *n* = 13) (WFVZ).

Mass of 2 fresh eggs 0.960 and 0.984 g (WFVZ). All the above data from eggs collected from Huachuca Mountains in southeastern Arizona. Eggs from Colorado measured 15.5 × 11.0 mm and 15.5 × 10.5 mm (*n* = 2; [56]).

Incubation

Only the female is known to incubate. Duration of incubation unknown, but probably between 15 and 19 d, as in other hummingbirds. No information on hatching.

Young Birds

No data for Rivoli's Hummingbird. Hatchlings altricial.

For the closely-related Talamanca Hummingbird, there is information for a single brood observed by F. G. Stiles in 1989 at 3,100 m on Cerro de la Muerte, Costa Rica. Nestlings located on 10 May at about 3–4 d of age, were ready to leave nest 31 May (i.e., nestling period is ≥ 25 d).

Parental Care

No information available.

Cooperative Breeding

Not applicable for this species.

Brood Parasitism

Not known to occur.

Fledgling Stage

No information available.

Immature Stage

Very few data. Juvenile Talamanca Hummingbirds in Costa Rica lose bill corrugations at about 5 months, when Preformative Molt begins (F. G. Stiles, personal communication). Rivoli's Hummingbird are presumably similar.

Demography and Populations

Measures of Breeding Activity

Age at First Breeding; Intervals Between Breeding

Most likely the first spring/summer after hatching. Males banded as juveniles in southeastern Arizona were captured the following June and July in full breeding plumage (DRP). No information on intervals between breeding.

Clutch

Few data. In the Huachuca Mountains of southeastern Arizona, clutches included 2 eggs (n> 10 nests) (112; unpublished data from several museum collections).

Annual and Lifetime Reproductive Success

No information available.

Number of Broods Normally Reared per Season

No information available.

Life Span and Survivorship

During a 7-year project in the Chiricahua Mountains of southeastern Arizona, no Rivoli's Hummingbird was recaptured more than 2 years after being banded. Most birds were at least 1-year old when banded, suggesting that they live to be at least 3-years old. The data were strongly biased toward males (nearly 5:1) because females do not tend to visit feeders as frequently or as regularly as males do. This was also the case at Ramsey Canyon in the Huachuca Mountains of southeastern Arizona, where only 60 of the 248 birds (76%) banded from 1991–1995 were males, with immature (second-year) males being the most common age-sex class (S. Williamson

and T. Wood, personal communication). See also Appearance: Plumages, and Molts. The oldest documented individuals have been a male of 11 yr, 2 mo and another male of 9 yr, 2 mo, both from Arizona (113).

Disease and Body Parasites

Few data. At Ramsey Canyon in southeastern Arizona, S. Williamson and T. Wood (personal communication) have observed louse eggs on rectrices on 21 April and 1 May, and a live louse on an immature (second-year) male on 28 April. They noted, however, that the presence of the live louse is rare.

Causes of Mortality

Very few data; susceptible to exhaustion, probably owing to lack of food. Since 1989, several males have been found in a weakened state on the ground in the Chiricahua Mountains of southeastern Arizona (DRP). After rest and feeding, most of these birds regained their ability to fly.

Range

Philopatry to breeding areas is probably high; e.g., from over 100 recaptures of banded birds, only 2 individuals were recaptured in another location (S. Williamson and T. Wood, personal communication; DRP). A male banded in Ramsey Canyon, Huachuca Mountains, Arizona, on 20 July 1987 was recaptured at Madera Canyon, Santa Rita Mountains, Arizona (approximately 55 km west of Ramsey Canyon) on 24 July 1992; this bird was recaptured 2 yr later back at Ramsey Canyon (S. Williamson and T. Wood, personal communication). A second male banded in Ramsey Canyon on 8 April 1993 was recaptured on 19 August 1993 in the Mogollon Mountains (approximately 240 km northeast of Ramsey Canyon; just east of Roberts Lake) in western New Mexico (W. Calder, unpublished data). Since 1991 at Ramsey Canyon, 41% of males (total banded = 188) and 23% of females (total banded = 60) have returned in subsequent years to that locale (S. Williamson and T. Wood, personal communication). Since 1989, 26% of males (total banded = 49) and no females (total banded = 14) that were banded as adults in the Chiricahua Mountains have been recaptured in subsequent years (DRP). These measurements are undoubtedly underestimates because of the transient nature of Rivoli's Hummingbird and the short duration of mist-netting efforts.

Population Status

Like other hummingbird species, Rivoli's Hummingbird is difficult to survey. It is rarely detected on North American Breeding Bird Survey routes. Between March and July 1995, there were 123 males captured in the Chiricahua Mountains, Arizona (E. Sandlin, personal communication); the total was greater than the number of Blue-throated Hummingbirds or Black-chinned Hummingbirds captured at the mist-netting location. At Ramsey Canyon Preserve from 1986–1994, the number of birds caught annually has ranged from a low of 31 in 1991 to a high of 100 in 1986 (S. Williamson and T. Wood, personal communication).

Population Regulation

Few data; needs study. As for most hummingbird species, food supply and extreme weather events are likely important factors.

Conservation and Management

Effects of Human Activity

Feeders offer an energy subsidy that can maintain unnaturally large populations in certain areas when natural food flowers are scarce (e.g., Chiricahua Mountains, Arizona, where many flowers do not bloom until the onset of monsoon rains in July). Because the range of the Rivoli's Hummingbird within the U.S. is restricted to higher elevations of small isolated mountain ranges, forest fires can severely restrict habitat availability over the short term. Habitat destruction in southern Mexico and Central America may have a longer-lasting impact on populations, but this has not been well studied.

Management

No information. No known management activities have been directed toward this species.

Other

Anatomy and Physiology

Circulatory System

Heart mass in 6 adult males in Chiricahua Mountains, Arizona averaged 0.25 g ± 0.03 SD (range 0.22–0.29), which is 3.3% ± 0.43 SD (range 2.84–3.92) of adult body mass (DRP).

Total Body Water

Percent total body water for 6 adult males in Chiricahua Mountains, Arizona averaged 63.4% ± 1.95 SD (range 59.60–65.06) (DRP).

Priorities for Future Research

Despite the extensive range and abundance of the Rivoli's Hummingbird, much about its basic life history remains unknown. These gaps in knowledge have been noted widely in the account, but are summarized here as follows: migration and movement ecology, breeding biology

(courtship, nest construction, number of broods, nestling development, parental care), breeding success, feeding behavior (dietary importance of insects; role of bill dimorphism in feeding efficiency), and the function of different vocalizations.

Acknowledgments

Original Account (1996)

Portions of my research have been supported by the National Aeronautics and Space Administration, National Geographic Society, George Fox University Faculty Development Fund, Holman Endowment for the Sciences (George Fox University), National Science Foundation (grants to Wesley W. Weathers and Bret W. Tobalske), and Agricultural Research Station (University of California, Davis). This manuscript has profited from the critiques of Robert S. Ridgely, Keith Russell, Alan Poole, and Peter Scott. A host of colleagues and assistants, including Amanda Braun, Ann Brice, Alison Brown, Paul Caron, Tim Conley, Phil Getsinger, Tom Greek, Erick Greene, Aaron Irish, Ann Kjemtrup, Todd McKee, Todd McWhorter, Sean Powers, Elizabeth Sandlin, Scott Smithson, Sandy Taylor, Bret Tobalske, Jessamyn Van Hook, Wes Weathers, Marcus Webster, and Ray Munson, have provided invaluable advice and technical assistance over the years. My sincere thanks to Wade Sherbrook and the staff and volunteers of the Southwestern Research Station for going out of their way to accommodate my needs. I am also grateful to Bill Baltosser, William Calder, Penny Ficken, Lloyd Kiff, Elizabeth Sandlin, Peter Scott, F. Gary Stiles, Sheri Williamson, Tom Wood, the Western Foundation of Vertebrate Zoology (WFVZ) and several museum curators for sharing unpublished data with me. In addition to WFVZ, data were provided by the Cornell Lab of Ornithology, Florida Museum of Natural History, Peabody Museum of Natural History (Yale University), and Slater Museum of Natural History (Puget Sound).

Revised Account (2018)

Peter Pyle contributed plumage and molt descriptions in the Appearance article and Michael Patten contributed text to the Systematics article. Andrew Spencer reviewed Sounds and Vocal Behavior content.

About the Author(s)

Donald R. Powers grew up in southern California where he earned a B.S. at Biola College. While at Biola College, Powers was greatly influenced by the teaching of Raphael R. Payne who nurtured in him a deeply rooted love of all aspects of nature, especially the world of birds. This work is dedicated to “Rafe” and the profound impact he has had on Powers's life. Powers's interests focused on hummingbirds while he was a student of George W. Cox at San Diego State University (M.S., 1982) and Wesley W. Weathers at the University of California, Davis (Ph.D., 1989). At both institutions, Powers studied various aspects of hummingbird breeding ecology, energetics, and water regulation. Powers is currently a professor of biology at George Fox

University in Newberg, Oregon, where he has taught since 1989. His research interests on hummingbirds includes flight energetics and biomechanics, and the physiological effects of climate change. E-mail: dpowers@georgefox.edu.