

### The Northern Limit of the Hummingbird Genus *Oreotrochilus* in South America

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The hummingbird genus *Oreotrochilus* is represented by populations living at high altitudes in the South American Andes from north-central Ecuador to south-central Chile and adjacent Argentina (Berlioz and Jouanin 1942, Zimmer 1951, Peters 1945, Carpenter 1976, Olrog 1978). Ecuadorian populations constitute a morphologically distinct, allopatric taxon, which is related to the northern-most Peruvian and Bolivian species, *O. estella*, but is characterized by largely blue-headed adult males and is often treated as a separate species, *Oreotrochilus chimborazo* (Vuilleumier and Simberloff 1980, but see Zimmer 1951: 40). The northern-most of the three Ecuadorian *O. chimborazo* taxa is assigned to *O. c. jamesoni* (Jardine 1849), previously recorded in the western Cordillera as far north as Mt. Pichincha and in the eastern Cordillera as far north as the Guamani Pass, just north of Mt. Antisana (Orces 1944, Peters 1945, Corley-Smith 1969, Vuilleumier 1976). We here report a northward range extension of birds presumed to be of the *jamesoni* form, a presumption based upon two independent sets of visual observations in the headwaters of the Rio Pantavi, Imbabura Province, in the Mt. Cotacachi-Mt. Yana Urco de Piñán portion of the western range, about 70 km north of Mt. Pichincha (see Fig. 1).

Ortiz-Crespo visited the area on 22 December 1975 and saw a female *Oreotrochilus* feeding at the flowers of an isolated thicket of *Chuquiraga insignis* HB (Compositae) amid clumps of paramo grasses at an elevation of 3,600 m. A second visit to the area by Bleiweiss on 23 June 1980 documented the presence of a population, which was then tentatively assigned to *jamesoni*; at that time two records of adult males, both showing the all-blue head characteristic of the taxon *jamesoni*, as well as two of females, were made at elevations of 3,550–3,650 m in open or protected stream ravines where *Chuquiraga* was common.

In Ecuador, *Oreotrochilus* populations are found only above an elevation of 3,500 m up through the highest vegetated zones to the snow line. North of Mt. Pichincha, the western Andes are insular with respect to appropriate *Oreotrochilus* habitats. The deep, arid gorge cut by the Rio Guayllabamba effectively isolates Pichincha from the Cotacachi-Yana Urco massif to the north, which in turn is separated from the high mountains farther north by the course of the upper Rio Mira running roughly parallel to the Rio Guayllabamba and from high elevations to the east by an extension of the inter-Andean valley running north-south in northern Ecuador (see Fig. 1). Thus, in terms of both horizontal distance and eco-

logical barriers, the range extension we record here is of biological significance.

These new records permit us to emphasize several facts about the biogeography of *Oreotrochilus* in general and of the Ecuadorian populations in particular. First, members of *Oreotrochilus* seem to occur in dry puna (cf. Vuilleumier and Simberloff 1980) or puna-like grassland habitat through much of their range. Our new record documents a paralleling between the distribution of *Oreotrochilus* and these habitats, because the Cotacachi-Yana Urco region is covered by dry, puna-like grassland. It should be pointed out, however, that *Oreotrochilus* apparently does occur in a variety of habitats, from dry, brushy slopes to wetter paramo, elsewhere in Ecuador (Vuilleumier 1967), so grassland habitat may not be a necessary condition for *Oreotrochilus* at its northern limits. Furthermore, the grasslands of Cotacachi-Yana Urco are frequently burned and heavily grazed by cattle throughout the year, and, therefore, it is difficult to say whether the presence of *Oreotrochilus* represents a recent invasion due to the creation of favorable conditions by man or is part of the historic pattern of differentiation of *O. chimborazo* in Ecuador. The presence of *O. c. jamesoni* at the Guamani Pass, the northern-most record for *Oreotrochilus* in the eastern Cordillera of Ecuador, has been suggested to result from the creation of favorable habitat due to human disturbance (Corley-Smith 1969). The Guamani Pass is an exceedingly wet site (Vuilleumier 1976), which might be unfavorable habitat for *Oreotrochilus* under natural conditions. Similarly, in the high-altitude regions immediately to the north of the presently revised western portion of the range, rainfall appears to be much greater than within the range (Ortiz-Crespo 1974). This additional correlation of *Oreotrochilus* distribution with climatic factors in western Ecuador, in light of the general ecology of the genus, suggests that *Oreotrochilus* is not a recent invader to the Cotacachi-Yana Urco region.

Also of interest is the co-occurrence of the plant *Chuquiraga* and *Oreotrochilus*. Ortiz-Crespo has never observed the birds feeding from plants other than *Chuquiraga insignis* in Ecuador, and the availability of this plant may be requisite for the presence of *Oreotrochilus* in the Ecuadorian part of its range. A high reliance of *Oreotrochilus* on *Chuquiraga* is corroborated by several other investigators. Corley-Smith (1969) also notes encountering *O. chimborazo* only in the presence of *Chuquiraga*, and Carpenter (1976) found, for some Peruvian populations of *O. estella*, an exclusive dependence on *Chuquiraga spi-*

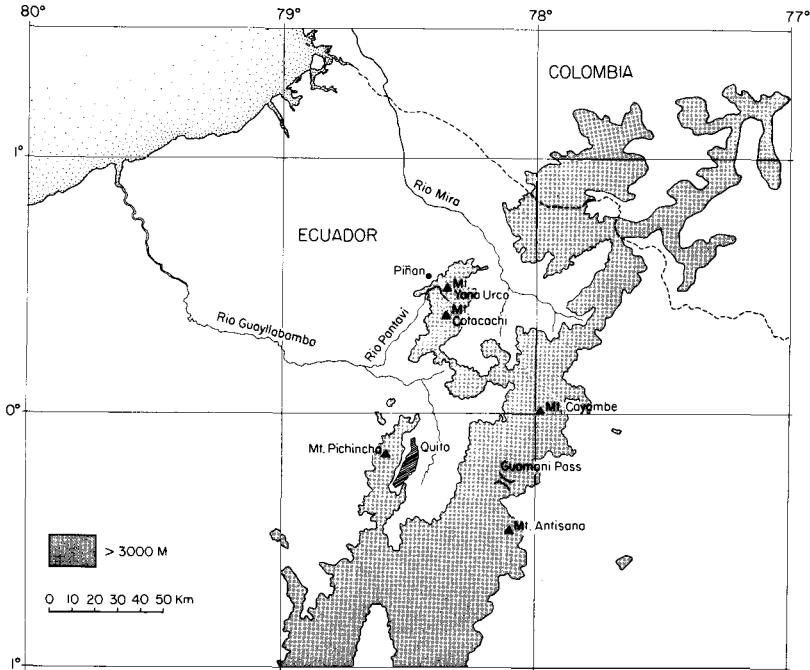


Fig. 1. Map of north-central Ecuador showing localities mentioned in the text.

*noza* as a native nectar source during the winter, nonbreeding season. Curiously, there are no *Oreotrochilus* records from Mt. Cayambe, the next major peak north of Mt. Antisana in the eastern Cordillera, although *Chuquiraga* occurs there (L. Holm-Nielson pers. comm. 1980). However, *Oreotrochilus* is also adapted in roosting, breeding, and other feeding habits to the vegetation and physiographic features of drier, high-altitude habitats (Carpenter 1976), and these factors may also influence distribution. The apparent absence of *Oreotrochilus* from the relatively undisturbed wet paramos of Mt. Cayambe may be due to these factors.

Our record of *Oreotrochilus* in the Cotacachi-Yana Urco area also points out a close parallel in the apparent northern terminus of this widespread genus with that of the Giant Hummingbird (*Patagona gigas*), another widespread species characteristic of the southern Andes. *Patagona* has previously been recorded on the Cotacachi-Yana Urco massif from the Lake Cuicocha area near Cotacachi (Ortiz-Crespo 1974), only 20 km south of our present record of *Oreotrochilus*. During Bleiweiss's visit, a single *P. gigas* was observed close to the *Oreotrochilus* populations, at 3,150 m on the west slope of Yana Urco, above Piñan, and the species was common east of this point on the west side of the inter-Andean valley. *P. gigas* differs ecologically from *Oreotrochilus*, occurring at lower elevations and in more xeric habitats, and the Guayllabamba canyon is apparently not a barrier for

this species (Ortiz-Crespo 1974). Both occur in drier habitats, however, and may be similarly limited further northward by the increased rainfall in northernmost Ecuador.

There is no reason to believe that the currently revised northern limit of *Oreotrochilus* is definitive. The range extension we record here, however, highlights some of the major features in the geographical ecology of this Andean hummingbird.

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### Differential Occurrence of Yearling and Adult Male Gadwalls in Pair Bonds

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Most age-specific information on breeding waterfowl has been concerned with the reproductive characteristics of females, and few data are available on the effects of age on male breeding biology. Weller (1964) and Lack (1968) have extensively reviewed the literature on breeding age in the Anatidae. Lack, in particular, noted that males of the Anatini, especially of the genus *Anas*, probably breed as yearlings. In the Athyini, a group in which a large excess of males compete for smaller numbers of females, drakes may not breed until the second breeding season. In the Mergini, most males take part in the breeding activities at the age of 3 (Lack 1968). As part of my research on the breeding ecology of the Gadwall (*Anas strepera*) in southern Manitoba, I obtained information on the age of paired males in order to evaluate the relationship of age to breeding activity.

During 1972-1975 at Delta and Marshy Point, Manitoba, I gathered data on 79 Gadwall pairs from observations following banding or directly from birds collected. All ducks were aged as yearlings (1 yr old) or adults (2 yr old or older) at the time of capture or collection (Blohm 1977).

In 39 cases, the ages of both pair members were known. Adult males were involved in 29 (74%) pair situations, while yearling males were involved in 10 (26%). In the 40 cases in which only the ages of males were available, adult drakes were present in 31 (78%) pair bonds, and yearling males were involved in the remaining 9 (22%). Adult male/adult female pairs (20 of 39, 51%) predominated over all possible sex-age combinations. Next in order of frequency were adult male/yearling female (9 of 39, 23%) and yearling male/yearling female (7 of 39, 18%) pair bonds. The

most infrequent combination was the yearling male/adult female category (3 of 39, 8%).

The importance of the observed frequencies cannot be evaluated without a consideration of the relative availability of young and adult males during pairing. In southern Manitoba, I found that most Gadwalls arrived already paired, and Paulus (1980), working on the ecology of Gadwalls on their wintering grounds, stated that most birds were already paired upon departure from Louisiana during late March-early April. Although the age structure of the Gadwall on wintering areas is unknown and not readily determined, a conservative approach is to determine the proportion of yearling males present during the breeding season, using general population projection models (see Martin et al. 1979: 214). For example, I used the following values [e.g. see Anderson 1975, Mallard (*Anas platyrhynchos*); Blandin in prep., Black Duck (*Anas rubripes*)] as reasonable mean parameter estimates for a dabbling duck population:

$S_{AM} = 0.60$  = average annual survival rate for adult males;

$S_{AF} = 0.55$  = average annual survival rate for adult females;

$S_{YM} = 0.45$  = average annual survival rate for young males;

$S_{YF} = 0.45$  = average annual survival rate for young females;

$R = 0.50$  = sex ratio of young birds expressed as proportion male;

$P = 2.0$  = average annual recruitment rate or pre-season age ratio (young/adult female in the fall population).

Accordingly, this modelling effort predicted a value of 0.40 as the asymptotic proportion of yearling males in a breeding-season population. Then, as-

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