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## On the dispersal of highland birds in tropical South and Central America

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## NOTAS GENERALES

### ON THE DISPERSAL OF HIGHLAND BIRDS IN TROPICAL SOUTH AND CENTRAL AMERICA

In order to explain similarities of the fauna of the isolated Sierra Nevada de Santa Marta of northern Colombia and that of the mountains of northern Venezuela Todd assumed the former existence of "an imposing mountain chain, comparable to the Andes in height even if not in extent, (which) must once have stretched along the northern coast of the South American continent, . . . , serving as a pathway over which many Subtropical and alticoline forms have traveled to reach their present stations" (Todd & Carriker, *Ann. Carnegie Mus.* 14: 106, 1922). Similarly, the mutual resemblance of the Subtropical bird faunas of the mountains of Colombia, eastern Panamá and Costa Rica was for Chapman (*Bull. Amer. Mus. Nat. Hist.* 36: 155-156, 1917) "conclusive proof of a former physical connection of the areas concerned, at which time this (Subtropical) zone stretched more or less continuously from northwestern Colombia through Panamá to Costa Rica". This supposed mountain system of Panamá "must have had an elevation of not less than five thousand feet". According to the same author the disappearance of these mountains was due to subsidence and erosion "at a comparatively recent period".

In general, there is no indication for large scale subsidence of whole mountain systems in northern South and southern Central America, but only evidence for continued differential uplift of these areas since late Tertiary time (although local sinking did probably occur in some regions). More specifically, the isolated "basement" highs on the outer Guajira Peninsula of northeastern Colombia and on the Dutch West Indian Islands used by Todd to reconstruct "an imposing mountain chain" were low islands in the Tertiary sea as shown, for example, by fringing reefs of Oligo-Miocene age and by younger offlapping sediments in the surrounding areas of the outer Guajira Peninsula (J. F. Rollins, *Univ. Nebraska Stud., new ser.*, 30, 1965, and personal observations). These Tertiary islands probably came into existence during the Upper Eocene. The highest elevation of approximately 800 meters is found in the Serranía de Macuira on the Guajira Peninsula and was reached through continued uplift during the late Tertiary and Pleistocene.

There is no geological evidence to support Chapman's assumption of a former high mountain connection of the Colombian Andes with the Cordilleras of western Panamá-Costa Rica as pointed out already by Griscom (Bull. Amer. Mus. Nat. Hist., 64: 61, 1932). This latter author (op. cit.: 63) held the alternative view that during maximum Pleistocene refrigeration "the avifauna of the Subtropical Zone in Central America descended to sea-level and had consequently a chance to pass continuously from Mexico to Colombia". However, it now seems probable that large parts of the present lowlands of Central and northern South America remained in the Tropical Zone even at the height of the Pleistocene refrigeration and were only affected by alternating dry and humid climatic periods (Haffer, Amer. Mus. Novit. 2294 : 1-57, 1967).

The following considerations may help to understand the Pleistocene dispersal of montane birds in the area under discussion:

1. Due to a possible *increase of the temperature gradient* in at least parts of the Tropics during the glacial periods of the Pleistocene (Haffer, loc. cit.) comparatively low hills of presently only 400 to 500 meters elevation may have had a subtropical summit during those periods. The Temperate Zone possibly extended down to 1400 or at times even to 1000 meters elevation (the latter figure depends on the validity of the exceptionally high Riss-glacial temperature depression of  $11^{\circ}\text{C}$  on the Bogotá plateau at an elevation of 2600 meters at the present time; van der Hammen & González, Leidse Geol. Med., 25: 306, 1960). Despite the lowering of the Pleistocene sea level by about 100 meters during the glacial periods (which resulted in a corresponding "increase" of present elevations) and the lowering of the altitudinal temperature zones complete continuity of the Subtropical Zone along the mountain ranges was probably not achieved. Small gaps in this temperature zone (average temperature from  $21^{\circ}$  to  $15^{\circ}\text{C}$ ) probably remained around Lake Nicaragua, in the Panamá Canal Zone and in the lower Atrato valley of northwestern Colombia. The Subtropical Zone of the table mountains of the Guiana Shield was probably widely separated from the Subtropical Zone of the Andes by the intervening tropical lowlands. However, low mountains of 500 to 700 meters elevation are found in the lowlands of eastern Colombia and possibly had a subtropical summit during the glacial periods.

2. It would seem possible that, during the glacial periods, many montane bird species had a relatively *wider vertical range with respect to altitudinal temperature zones* than they have today. The tropical lowlands were somewhat cooler and more humid during the glacial periods (increased rainfall and decreased evaporation due to more continuous cloud cover). For this reason many montane species possibly extended their range down the mountain slope where ecological conditions, though still tropical, somewhat ap-

proached those of their Subtropical home. After the return of warmer and less humid conditions, such as today, these species became again restricted to the higher mountain level of the present Subtropical Zone. Because of the extended vertical range of many montane species during the glacial periods I assume their horizontal range was more or less continuous across the gaps in the Subtropical temperature zone mentioned above (cf. Griscom, op. cit.).

3. A number of highland birds, particularly those of the Temperate and Páramo Zone, probably reached isolated mountain massifs by "hopping" across the intervening tropical lowlands (Stresemann, J. Orn. 87: 380 ff., 1939; Mayr & Phelps, Jr., Acta XI Congr. Int. Orn., p. 399, 1955), using available low mountains as stepping stones. On the other hand many species were unable to cross the gaps in their respective life zone. Due to the greater distances between mountains sufficiently high to carry faunas of the Temperate and Páramo Zone, even during the glacial periods of the Pleistocene, dispersal by hopping across the lowlands and/or lower mountains was more difficult and occurred less frequently. Consequently, endemism is more common among birds of the higher life zones of isolated mountains.

It is concluded that the dispersal of highland bird species in tropical South and Central America probably took place under presently existing orographic conditions. There is no ornithological need and much less geological evidence for continuous mountain bridges connecting isolated Andean mountain massifs of these regions during past geological periods. — JÜRGEN HAFFER, *Colombian Petroleum Co., Apartado Aéreo 3434, Bogotá, Colombia, 15 July 1966. Present address: Mobil Oil Corporation, Field Research Laboratory, P.O. Box 900, Dallas, Texas 75221, U.S.A.*

#### INTERSPECIFIC COMPETITION AS A POSSIBLE FACTOR IN LIMITING THE RANGE OF SOME TRANS-ANDEAN FOREST BIRDS

Speciation is fully completed if reproductive isolation and ecologic compatibility have been attained by two populations during geographic separation. In case such isolated populations come in secondary contact after reproductive isolation was completed but before sufficient ecologic differences were developed, both will compete and may inhabit mutually exclusive areas in which each form presumably is at a competitive advantage over its ally. The following cases among birds inhabiting the forests west of the Andes may belong here:

*Tangara gyrola* - *T. lavinia*: *Tangara gyrola* inhabits tropical South America north to Costa Rica. It is widespread in the Amazonian lowlands. However, in the northwestern part of its range this species is confined to the