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PATTERNS OF ELEVATIONAL AND LATITUDINAL DISTRIBUTION, INCLUDING A "NICHE SWITCH," IN SOME GUANS (CRACIDAE) OF THE ANDES[1]

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Abstract. A recently discovered population of *Chamaepetes goudotii* (Sickle-winged Guan) in the eastern Andes of southern Peru and northern Bolivia is anomalous in its high-elevation (above 3,000 m) distribution; populations from central Peru to northern Colombia are found generally below 2,100 m. Several hypotheses are evaluated to account for the origin of such an unusual distribution. No evidence for long-distance dispersal or human introduction was found (and previous claims of introduction by ancient civilizations to account for disjunct distributions of two other species of New World birds are disputed). We propose that the current pattern is the result of fragmentation of a once continuous distribution. Hypotheses concerning the cause of the fragmentation and maintenance of the current pattern are evaluated. The relative consistency of elevational distributions of Andean bird species over broad latitudinal ranges (and dramatic differences in species composition with changes in elevation) provides circumstantial evidence against an autecological hypothesis that would propose that ecological requirements are met for *C. goudotii* only in the two disjunct regions. If potential competitors are restricted to congeners, no support can be found for a hypothesis based on interspecific competition. However, if the field of potential competitors is expanded to include morphologically similar confamilials, a striking pattern of generally nonoverlapping distributions in terms of elevation and latitude is revealed. Most striking is the reversal in elevations occupied by *C. goudotii* and *Penelope montagnii.* The reliance on interpretation for evaluating competing hypotheses makes such analyses inherently unsatisfying.

Key words: Guans; Andes; Penelope; Chamaepetes; *patterns of distribution; interspecific competition.*

INTRODUCTION

Three specimens of the Sickle-winged Guan (*Chamaepetes goudotii*) collected by Cardiff in humid Temperate Zone forest of Dpto. La Paz, Bolivia, in June 1980 represented an 800-km southerly range extension and established the first records for Bolivia (Cardiff and Remsen 1981). Such a range extension was not entirely surprising because recent fieldwork in the forested Andes of northwestern Bolivia has produced 12 new species for Bolivia previously unrecorded south of central or southern Peru (Parker et al. 1980, Cardiff and Remsen 1981, Schulenberg and Remsen 1982, Remsen and Traylor 1983) despite visits by several earlier workers (including M. A. Carriker, who spent 12 days at Hichuloma, at the same elevation as, and only 2 km from, the guan locality). It was a surprise, however, that a cracid would pass undetected for so long, only 2 hr on the main road from the city of La Paz. Cracids are almost always familiar to native inhabitants and are among the first birds acquired for collectors by local hunters or mentioned when inquiring about the local avifauna. Thus, the discovery of this population resembles the rediscovery of the White-winged Guan (*Penelope albipennis*) within sight of the Pan-American Highway in Peru (Williams 1980). Both cases illustrate that the distributional limits of many South American birds are still not well established.

Although this major extension in latitudinal distribution for *C. goudotii* was of zoogeographic interest, the *elevation* at which the Bolivian population was discovered was more significant. Throughout its range in the Eastern Andes from Colombia to central Peru, *C. goudotii* occurs at low elevations, usually below 2,100 m. Yet the newly discovered southern populations, including additional specimens collected subsequently in Dpto. La Paz (Remsen 1985) and Dpto. Puno, southern Peru (specimens at Museum of Natural Science, Louisiana State University, LSUMNS) were found 1,000 m higher, at 3,000–3,300 m.

Such a dramatic latitudinal switch in elevational range is unusual in Andean forest birds,

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most of which occur within relatively consistent elevational limits throughout most of their latitudinal range (Chapman 1926, Graves 1985, LSUMNS specimens, pers. observ.). In this paper, we first describe the pattern of elevational distribution of *C. goudotii* and other guans (Cracidae) of the Andes, and then attempt to determine why this species shows such an odd pattern of distribution.

METHODS

Specimen localities for montane guans were obtained from museums with major collections of Andean birds (see Acknowledgments). We feel that we located most guan specimens with locality data sufficiently precise to allow plotting of latitude and elevation. Latitudes were taken primarily from the ornithological gazetteers of the Andean countries (Paynter et al. 1975; Paynter and Traylor 1977, 1981; Paynter 1982; Stephens and Traylor 1983). If the specimen label did not include elevation, the gazetteers were used to determine if the elevation could be ascertained with reasonable precision. A substantial number of specimens could not be used because their elevations could not be determined. For specimens for which the elevation was given as a range, e.g., "2000–2400 m," the midpoint of the range was used as the elevation, unless the specimen was from near an upper or lower limit of the species' overall elevational distribution, in which case the specimen was not used.

RESULTS AND DISCUSSION

A plot of specimen localities of *C. goudotii* on the eastern slope of the Eastern Andes (Fig. 1) reveals that the species' elevational distribution switches dramatically from below 2,100 m to above 3,000 m at about 11°S. We are certain that the high-elevation population does not represent wandering or migratory individuals: guans are sedentary birds, with no known cases of long-distance movement or vagrancy (Delacour and Amadon 1973).

Whether the observed pattern is a sampling artifact, however, deserves consideration. Although *C. goudotii* can be locally common (Johnson and Hilty 1976), it usually occurs in low densities, and this probably plays a more important role than shyness in determining whether or not it is recorded at a site. Some members of a field party may never see the bird over a period of weeks, even though seen several times by coworkers, and some expeditions may not record the species at all but then find it on return visits.

Nevertheless, we are reasonably certain that *C. goudotii* does not occur at elevations below approximately 2,800 m south of 11°S. Since 1979, approximately 190 person-days have been spent by personnel of the Museum of Natural Science, Louisiana State University, in humid forest above 3,000 m in the area occupied by the newly discovered, high-elevation population of *C. goudotii* (see Cardiff and Remsen 1981 and Remsen 1985 for localities in La Paz; the locality in Dpto. Puno, Peru, is "Valcon, 5 km NNW of Quiaca, 3000 m," 6–18 October 1980). This effort produced seven specimens and several sight records. By comparison, approximately 220 person-days have been invested at the same latitudes but below 2,600 m in La Paz and Puno without recording *C. goudotii* (2,575 m, Sacramento Alto, 8 km by road north Chuspipata, Dpto. La Paz, Bolivia, 20 July–8 August 1979; 2,000 m, Abra de Maruncunca, 10 km southwest of San Jose del Oro, Dpto. Puno, Peru, 9 November–6 December 1980; 1,650 and 1,350 m, Serranía Bellavista, 35–36 and 47 km, respectively, by road north of Caranavi, Dpto. La Paz, Bolivia, 10 June–2 July 1979 and 10 July–2 August 1980, respectively). Therefore, we believe that the unusually high and compressed elevational range of the newly discovered southern population is not a sampling artifact.

We are even more certain that *C. goudotii* does not occur above 2,300 m elevation north of 11°S. LSUMNS expeditions in central and northern Peru have logged over 500 person-days in humid forest above 2,300 m without finding any *C. goudotii.*

What processes would produce this elevational switch? What factors maintain the present pattern of limits of distribution? These zoogeographical questions are difficult to answer because (a) the historical processes can never be ascertained with complete certainty, leaving inference as the primary methodology, and (b) experiments to test hypotheses concerning large-scale distribution patterns are usually logistically intractable, especially for flying birds (Diamond 1986a). The remainder of this paper represents our attempt to answer these questions for *C. goudotii.*

We considered three hypotheses concerning the process that might account for this unusual elevational "niche switch" pattern of distribution:

(1) long-distance dispersal, (2) human introduction, and (3) vicariance. We then considered two hypotheses that might explain how such an unusual pattern might be maintained: (1) autecology and (2) interspecific competition.

HISTORICAL HYPOTHESES

LONG-DISTANCE DISPERSAL

One hypothesis that might account for the current disjunct pattern of distribution is that it was the result of long-distance dispersal. In other words, perhaps some individuals dispersing long distances from one area successfully colonized the other without colonizing intermediate areas.

We find no support for long-distance dispersal for two reasons. First, the gaps in the distribution of *C. goudotii* do not correspond to gaps in current habitat availability. The areas from which the species is absent are all filled with seemingly appropriate habitat (humid montane cloud-forest) that is occupied by bird assemblages typical of such habitat. Only a few, narrow, arid canyons (e.g., the Marañon and Urubamba valleys) interrupt an otherwise continuous blanket of montane forest from Venezuela to central Bolivia. Therefore, a dispersal hypothesis requires special pleading to explain why these intermediate areas have not been colonized by gradual expansion from either or both directions. Second, guans are perhaps the least likely long-distance dispersers among the generally sedentary Andean forest birds. All cracids fly poorly and are probably incapable of lengthy flight; *C. goudotii* is typical of guans in this respect (pers. observ.). We cannot rule out the possibility that a group of guans dispersed by walking or by a series of short flights across hundreds of kilometers of habitable forest to colonize forest nearly 1,000 m above or below their normal elevational distribution without colonizing intervening elevations or latitudes. This prospect, however, must be viewed as extremely unlikely for birds for which there are no instances of extralimital occurrences.

INTRODUCTION BY HUMANS

Haemig (1978, 1979) proposed that introduction by primitive peoples accounts for the anomalous, disjunct distributions of two species of Mexican birds, the Great-tailed Grackle (*Quiscalus mexicanus*) and the Tufted Jay (*Cyanocorax dickeyi*). The analogous hypothesis here would propose that one of the elevationally disjunct populations of *C. goudotii* was deliberately or accidentally introduced by primitive peoples. Because guans are potential sources of food for humans, this hypothesis deserves special consideration.

A thorough evaluation of the human introduction hypothesis would require extensive, original research on the anthropology and archaeology of the region. Such an analysis is beyond our expertise. In our opinion, however, introduction by humans seems unlikely for two reasons. First, the human population density of the humid, forested Eastern Andes is currently, and probably always has been, relatively low. The steepness of the slopes, the high degree of cloud cover, and, at upper elevations, the cold temperatures all make this region unfavorable for agriculture. So, the region in general does not seem to have been a likely area for intensive human activity. Second, efforts at domesticating cracids have remained largely untried owing to their low clutch size and aggressive behavior toward conspecifics, thereby requiring relatively large enclosures (J. P. O'Neill, pers. comm.). That cracids are not ideal for domestication, however, does not preclude their transport as cagebirds from place to place by primitive societies.

We also are not convinced that Haemig's (1978, 1979) cases of proposed human introduction are valid. The disjunct distribution patterns of *C. dickeyi* and *Q. mexicanus* are not nearly the zoogeographic anomalies that Haemig believed. *Cyanocorax dickeyi* belongs to a superspecies of blue/black-and-white jays, the members of which are distributed in a disjunct, relictual pattern in dry habitats in South America (Goodwin 1976); *C. dickeyi* is simply the most isolated of these taxa. At least four other taxa (Killdeer (*Charadrius vociferus*), White-winged Dove (*Zenaida asiatica*), Cave Swallow (*Petrochelidon fulva*), and the *Dives* superspecies of blackbirds show distribution patterns similar in some ways to that of *C. dickeyi* and its apparent closest relative, *C. mystacalis.* In all four cases, a taxon in the dry lowlands of the Pacific coast of South America has a sister taxon in Middle America. Other examples of taxa found in Middle America with relatives isolated in arid northwestern Peru-southwestern Ecuador are: (1) *Aimophila* spp. and *A. stolzmanni,* (2) *Tachycineta albilinea albilinea* and *T. a. stolzmanni,* and (3) *Forpus cyanopygius* and *F. coelestis.* The comparability of these distribution patterns depends on knowing the phylogenies of the taxa involved, including whether the two jays are sister taxa; these relationships are currently unknown. In our opinion, the only anomaly in the *Cyanocorax* case is not the disjunction itself but that the Middle American representative shows such a restricted distribution.

As for the isolated, high elevation population of *Q. mexicanus,* similar disjunct, montane valley populations of primarily lowland species are found in several places in the Western Hemisphere, particularly in the savanna region of Bogotá, Colombia, and the intermontane valleys of central Bolivia. The Mexican plateau region inhabited by the grackle is also inhabited by disjunct, highland populations of normally lowland species (e.g., Little Blue Heron *Egretta caerulea,* American Bittern *Botaurus lentiginosus,* Redhead *Aythya americana,* Ruddy Duck *Oxyura jamaicensis,* Yellow Rail *Coturnicops noveboracensis,* Virginia Rail *Rallus limicola,* Clapper Rail *Rallus longirostris,* Northern Jacana *Jacana spinosa,* Sedge Wren *Cistothorus platensis,* Marsh Wren *C. palustris,* Song Sparrow *Melospiza melodia,* and Red-winged Blackbird *Agelaius* {*phoeniceus*} *gubernator* [Moore 1945; Dickerman 1966; Ripley 1977; Banks and Dickerman 1978; AOU 1983; Williams 1989; S. O. Williams, in litt.]) for which a hypothesis of human introduction is untenable. Like the grackle, almost all these species are associated with aquatic or marshy habitats, as was the extinct *Quiscalus palustris.*

Furthermore, blackbirds (Icteridae) are notoriously adept at colonizing areas modified by human activity (Orians 1985). In particular, the Great-tailed Grackle has expanded its range dramatically within the last 50 years (Pratt et al. 1977, Garrett and Dunn 1981, Holmes et al. 1985). Therefore, we feel that both of Haemig's examples are readily explained within the context of broader distribution patterns, and that there is no need to invoke human intervention.

Concerning Haemig's data in support of human introduction, we note that it is entirely circumstantial and speculative in the case of the jay; in fact, Phillips (1986) dismissed Haemig's hypothesis outright. In the case of the grackle, the direct evidence comes from a friar's 1577 collection of animal stories told to him by Aztec informants (and not the friar's direct observations). Although the plausibility and detail of the latter are intriguing, we regard such folklore with distrust. Our personal experience with South American indigenous peoples as well as with "educated" peoples is sprinkled with cases of amusing, but obviously erroneous, explanations of past and present natural phenomena, in spite of detailed and accurate knowledge of natural history in other cases.

RELICTUAL DISTRIBUTION

The relictual distribution hypothesis would explain the disjunct distribution of *C. goudotii* by proposing that the once continuous distribution became fragmented by extirpation in portions of the range. A direct test of this hypothesis would require documentation of former presence or absence of *C. goudotii* in the current elevational and latitudinal gaps in its range. In the absence of an extensive fossil record from the eastern slopes of the Andes, evaluation of this hypothesis is not possible. We can find no evidence of historical change in the distribution of *C. goudotii* within the brief period of scientific sampling of Andean birds, roughly the last 100 years, although the failure of previous workers to find the southern population might be interpreted this way.

Nevertheless, we favor the relictual distribution hypothesis by default. Although we cannot provide direct evidence for once-continuous distribution followed by subsequent extinction in some areas, we believe that this best accounts for the current disjunct pattern because we have a plausible mechanism for the extinction of populations in the gaps (see below).

ECOLOGICAL HYPOTHESES

AUTECOLOGY

The two disjunct regions inhabited by *C. goudotii* might be the only two in which its ecological requirements are met. This hypothesis would propose, therefore, that this species can survive only at 3,000–3,300 m in southern Peru and Bolivia, and at 500–2,200 m from central Peru to Colombia.

Although our fragmentary knowledge of the biology of *C. goudotii* does not permit strong tests of such an hypothesis, available data do not support it. We find it difficult to believe that the cold, stunted forest near timberline in the southern Andes is in some critical aspect more similar to the warm, tall, lower montane forest in central Peru than either area is to immediately adjacent areas with similar habitat and climate. No other species of Andean bird shows a pattern similar to that of *C. goudotii.* Indirect evidence for ecological dissimilarity between the high- and low-elevation regions occupied by the disjunct *C. goudotii* populations comes from analysis of shared species. Of the resident bird species at the *C. goudotii* locality at 3,050 m in La Paz, Bolivia (Remsen 1985), 70 species occur 1,100 km to the north in Dpto. Huánuco, where *C. goudotii* is a low-elevation species. Of these 70 shared species, only 24 (34%) also occur at the uppermost locality for low-elevation populations of *C. goudotii,* at 2,100 m in Dpto. Huánuco (LSUMNS specimens). All 24 of the species found at 2,100 m are basically high-elevation species near the lower limit of their elevational range; all also occur at 3,050 m in Dpto. Huánuco. Only one of the 70 shared species occurs as low as the lower elevational limit of *C. goudotii,* at about 1,000 m. To illustrate further the latitudinal stability of community composition at a given elevation in the Andes, our comparison of the resident avifauna at 3,050 m in Dpto. La Paz with the species composition at the same elevation at a locality (Cordillera Colán; LSUMNS specimen data) much further north than Huánuco (1,700 km northwest of La Paz in extreme northern Dpto. Amazonas, Peru) revealed that 54 species and seven additional allospecies replacements are shared. This reflects a general pattern among Andean forest birds (and montane forest avifaunas in general): similar elevations support a similar species composition over a broad latitudinal range, but localities a few hundred meters apart in elevation tend to support different avifaunas (Terborgh and Weske 1975, Parker et al. 1985).

Because no other species of Andean forest bird shows a similar niche switch, and because very few species are shared by the two disparate regions occupied by *C. goudotii,* we are unable to construct a plausible reason why the two *C. goudotii* populations are found only where they are. Of course, until the biology of the species is better known, we will never be able to eliminate the possibility that some critical food plant, nest site, etc., is present only in the two disjunct regions, or that some species-specific, unconquerable parasite or predator is found everywhere but the two regions. As noted by Connor and Bowers (1987), a mosaic distribution such as that shown by these guans could also be produced or maintained by a comparable mosaic distribution of ecological requirements. Nevertheless, we maintain that the overall environmental dissimilarity between the two regions makes such a possibility unlikely.

If the elevational distribution of *C. goudotii* showed some gradual latitudinal change in the direction of increasing elevation with increasing distance from the equator, such a pattern could be used as circumstantial evidence for the autecology hypothesis, which would predict that changing elevational distribution is a response to some clinally varying climatic or ecological parameter. The locality data, however, do not show such a pattern. South of the equator, elevational limits appear to be more or less constant (Fig. 1), and the switch to high elevations takes place rather abruptly. Unfortunately, the poor resolution of the locality data prevents determination of whether the elevational shift occurs, as we suspect, on opposite sides of a major Andean river canyon. Given such a shift, the autecology hypothesis would require major climatological or ecological differences on opposite canyon sides, an unlikely possibility that nonetheless cannot be excluded at present.

If the latitudinal boundaries between guan taxa are formed by dry canyons that might be barriers to dispersal, then these barriers could maintain the current, parapatric pattern of distribution without invoking other factors. However, there are no barriers to dispersal across *elevational* boundaries—these boundaries must be maintained by some ongoing, ecological process.

The elevational niche switch poses the greatest difficulty for proposing that autecology is this ongoing process. It seems unlikely that a species that occurs at lower elevations throughout most of its distribution would suddenly find these lower elevations unsuitable in one section of its distribution while finding upper elevations suitable. That the reverse would occur in another guan, *Penelope montagnii,* in a geographically coincident manner compounds the unlikelihood of such a scheme (see next section).

INTERSPECIFIC COMPETITION

Perhaps *C. goudotii* is restricted to two disjunct areas because it is prevented from occupying the intervening geographic areas and elevations by competition with other species. Terborgh and Weske (1975) used a natural experiment, a mountain range isolated from the main Andes, to examine factors responsible for limiting the elevational distributions of Andean birds. They concluded that as many as two-thirds of the spe-

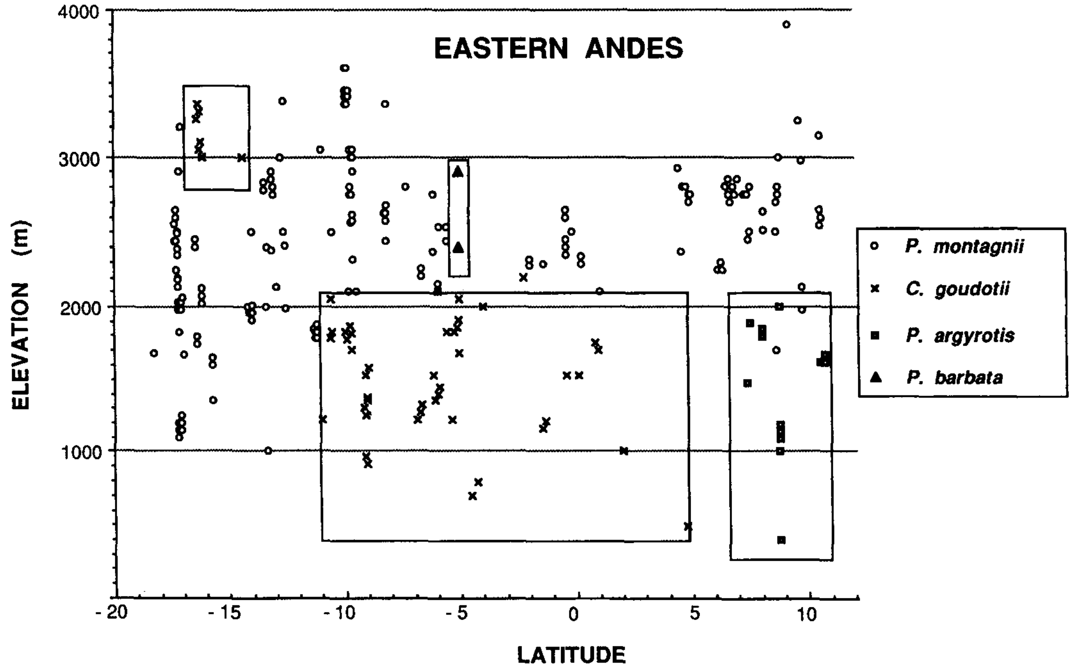

FIGURE 1. Specimen localities of five species of montane guans in the Eastern Andes from northern Venezuela and Colombia to northern Argentina. Each point represents a single specimen; when these are from precisely the same locality, the points are offset slightly but contiguous (also applies to Figs. 2–4). Latitudes range from central Bolivia to northern Venezuela; latitudes south of the equator are indicated by negative numbers.

cies' ranges were influenced by interspecific competition and that many of the presumed competitors were not congeners.

If one were to examine this hypothesis in the manner frequently used by community ecologists, namely to examine the distribution of congeners, the interspecific competition hypothesis is not supported for *C. goudotii*. The only other species in the genus *Chamaepetes* is the Black Guan (*C. unicolor*), found in the mountains of Costa Rica and Panama (Delacour and Amadon 1973). If, however, one examines other species of guans in the Andes, a pattern emerges that is consistent with the interspecific competition hypothesis.

A plot of elevation and latitude for guan specimens from the Eastern Andes (Fig. 1) shows the following features. First, although there is some overlap among various species, the pattern that is most evident is that the two most widespread species, the Andean Guan (*Penelope montagnii*) and *C. goudotii*, replace each other at approximately 2,100 m from central Colombia to southern Peru. However, from about 11°S to about 16°30′S, apparently from the Río Apurímac to the Río La Paz, their elevational relationship is reversed, with the recently discovered population of *C. goudotii* not known from below 3,000 m. This switch in elevational distribution apparently corresponds with subspecies boundaries in *P. montagnii*, but does not in *C. goudotii*. The southernmost subspecies of *C. goudotii*, *C. g. rufiventris*, ranges from Dpto. Huánuco to Dpto. La Paz, Bolivia, thus bridging the elevational switch (Cardiff and Remsen, unpubl. data).

Chamaepetes goudotii has not been recorded south of 16°30′S, in spite of intensive collecting in Dpto. Cochabamba, where *P. montagnii* occurs as high as 3,200 m. Farther south, the Red-faced Guan (*P. dabbenei*) replaces *P. montagnii* (contra Delacour and Amadon 1973) from Dpto. Tarija, Bolivia, south to Prov. Salta, Argentina; in fact, *dabbenei* is treated as a subspecies of *montagnii* by some authors (Olrog 1960, Vuilleumier 1965; cf. Vaurie 1967). The records of *P. montagnii* from Salta (Olrog 1960; Vaurie 1967, 1968) pertain to misidentified specimens of *P. dabbenei* (M. Nores, in litt.). Elsewhere in

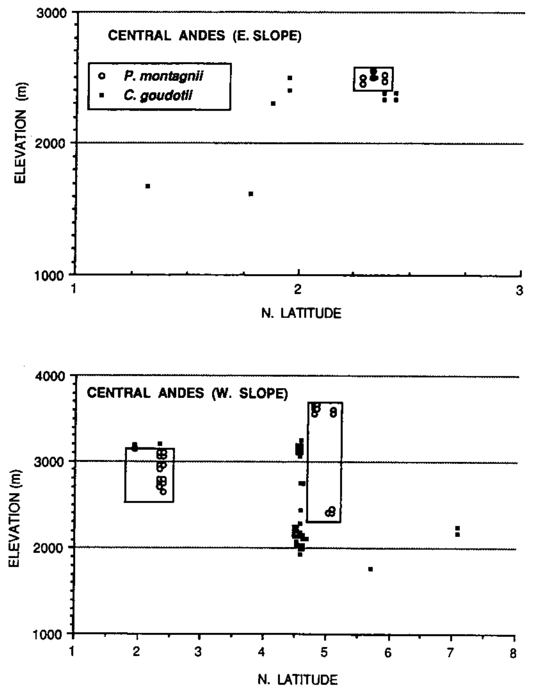

FIGURE 2. Specimen records of two species of guans on the eastern slope and western slope of the Central Andes of Colombia. Boxes enclose localities for *Penelope montagnii.*

the Eastern Andes, the Bearded Guan (*P. barbata*) is known from two localities, in extreme northern Peru in an area where *P. montagnii* does not occur (Parker et al. 1985). At the extreme north end of the Andes in northern Colombia and Venezuela, the Band-tailed Guan (*P. argyrotis*) occurs at elevations inhabited by *C. goudotii* farther south and below elevations typically inhabited by *P. montagnii.*

On the eastern slope of the Central Andes of Colombia (Fig. 2), *C. goudotii* has been collected from about 1,600 to about 2,600 m. *Penelope montagnii* has been collected only at 2,500–2,600 m at three northern localities. With so few localities, little can be said except that the two species have not been collected at the same locality and that *C. goudotii* is more widespread and may occupy elevations generally below those occupied by *P. montagnii.* On the western slope of the Central Andes (Fig. 2), the same tentative conclusions apply except that in the south, the few specimen records available suggest that *C. goudotii* occurs above *P. montagnii.* Because virtually all locality data from the Central Andes come from specimens taken 50–60 years ago, before the advent of accurate mapping of elevational distributions, we believe that all locality data from this region should be interpreted with

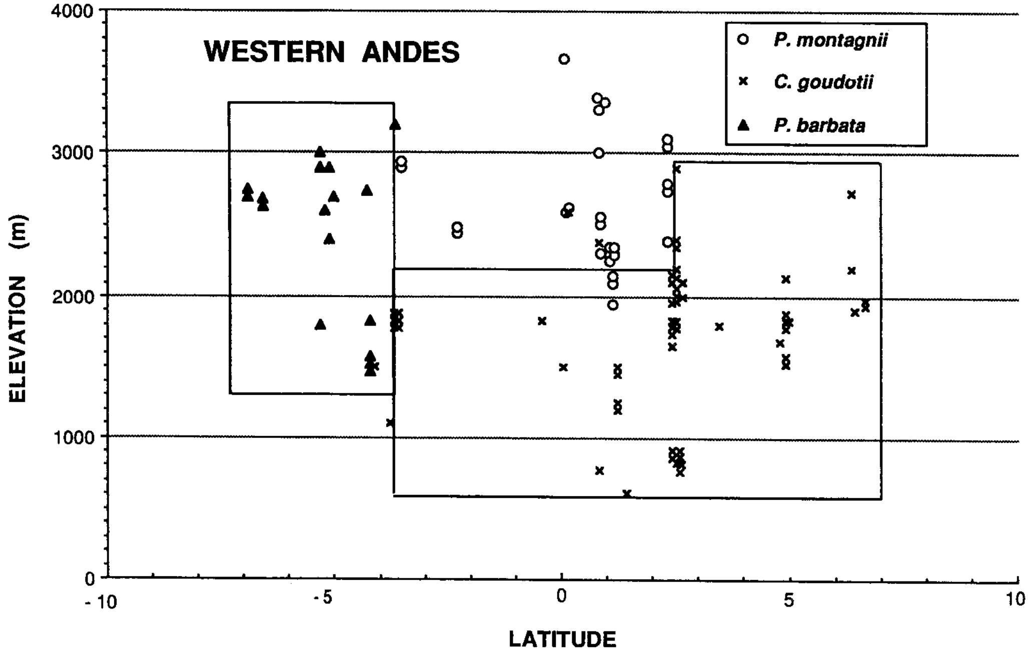

FIGURE 3. Specimen records of three species of guans in the Western Andes of Colombia, Ecuador, and northwestern Peru. Latitudes south of the equator are indicated by negative numbers.

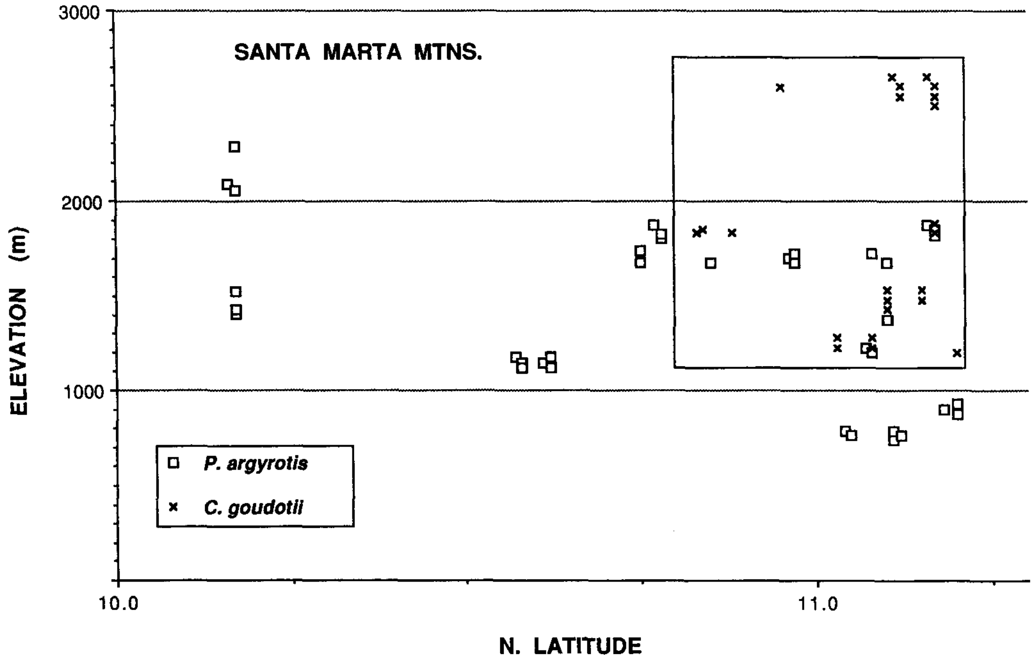

FIGURE 4. Specimen records of two species of guans in the Santa Marta Mountains of northeastern Colombia.

caution. Furthermore, throughout the Andes many professional collectors apparently ranged hundreds of meters above or below a given collecting locality, yet all specimens bore the same locality name.

In the Western Andes (Fig. 3), *C. goudotii* generally occurs below elevations occupied by *P. montagnii* in Ecuador and Colombia, with some elevational overlap; however, at only one locality have both species been collected. Neither species occurs south of about 4°30′S, where *P. barbata* occurs exclusively and occupies both the high elevations typical of *P. montagnii* and the low elevations typical of *C. goudotii.*

In the Santa Marta Mountains, an isolated, major mountain range in northern Colombia, two species of guans occur, *C. goudotii* and *P. argyrotis* (Fig. 4). Although Todd and Carriker (1922) reported that the two species overlapped broadly in elevational distribution, a plot of specimen localities (Fig. 4) shows that on the southern side of the Santa Martas, only *P. argyrotis* occurs, and *C. goudotii* is found only on the northern side. There, however, it does overlap broadly in elevational distribution with *P. argyrotis* but generally occurs above it. The two species have been collected together at five localities, but whether or not they are truly syntopic is unknown. In the Coastal Range of Venezuela (not mapped), where *C. goudotii* does not occur, *P. argyrotis* occupies all elevations from 300 m to the summits at ca. 2,000 m (Schafer and Phelps 1954).

Therefore, the general pattern throughout the Andes is that only one species of *Penelope* or *Chamaepetes* occurs at most, but not all, localities, and that *C. goudotii* occurs below one of the three species of *Penelope,* except in extreme southern Peru and northern Bolivia, where the situation is reversed. Although such a "repulsed" pattern of species' distributions is consistent with the predictions of the interspecific competition hypothesis, it is also consistent with other hypotheses that propose a parapatric distribution of autecological factors, such as habitat suitability, predation, and diseases (Connor and Bowers 1987).

With only a cursory knowledge of the ecologies of guans of the Andes, it is difficult to know whether these species are likely to be competitors. Examination of available data, however, favors consideration of all guan species as potential competitors. All are similar in overall size and proportions, especially in bill length (Table

FIGURE 5. UPGMA phenogram of five species of guans of the Andes. Species of three other genera of Cracidae are also included for comparison. Characters used were wing length, bill length, tarsus length, and tail length of adult males; measurements were taken from Vaurie (1968). Cophenetic correlation = 0.981.

1); *C. goudotii* has a disproportionately shorter tarsus, but is otherwise similar to *Penelope* spp. in size and shape. In fact, a phenogram based on wing, tail, tarsus, and bill measurements (Fig. 5) shows that all subspecies of *C. goudotii* are phenotypically more similar to some forms of *Penelope* than are some *Penelope* species to each other. Also, we can find no conclusive evidence to support the inferences of Todd and Carriker (1922) that *C. goudotii* is more terrestrial than *Penelope* (*P. argyrotis colombiana* in this case). On the contrary, Johnson and Hilty (1976) found that in the Santa Marta Mountains *C. goudotii* forages only in arboreal situations, although it regularly descends to the ground to cross open spaces.

TABLE 1. Measurements of some guans of the Andes. All measurements are lengths rounded to nearest 1 mm for adult males and are taken from Vaurie (1968). The largest and smallest subspecies of *Penelope montagnii* and *Chamaepetes goudotii* are included to encompass the range in variation in these two species.

Species (*n*)	Wing	Tail	Tarsus	Bill
Penelope argyrotis (21)	276	257	53	27
Penelope barbata (6)	261	257	57	28
Penelope montagnii plumosa (16)	240	233	54	27
P. m. sclateri (19)	263	240	57	26
Penelope dabbenei (7)	303	301	68	27
Chamaepetes goudotii fagani (16)	241	205	58	28
C. g. rufiventris (2)	269	255	66	28

Stomach contents are available only for *C. goudotii* and *P. montagnii.* Examination of these shows that both species' diets are roughly similar, with fruits in the 1–10 mm size range and other vegetable matter predominating in both (Fig. 6). Foraging observations for both these species and *P. barbata* (T. A. Parker, pers. observ.) indicate that they feed on small fruits taken primarily in trees. Thus, our ecological data, admittedly weak, are consistent with potential interspecific competition between *C. goudotii* and *P. montagnii.*

Not included in our analysis was the Wattled Guan (*Aburria aburri*), which overlaps broadly in latitudinal and elevational (600–2,500 m) distribution with various *Penelope* species and *C. goudotii.* If and how it differs ecologically from other montane guans is not known.

Although information on the distribution, ecology, and morphology of guans of the Andes is most consistent with the interspecific competition hypothesis, such an interpretation creates problems in terms of "common sense" nat-

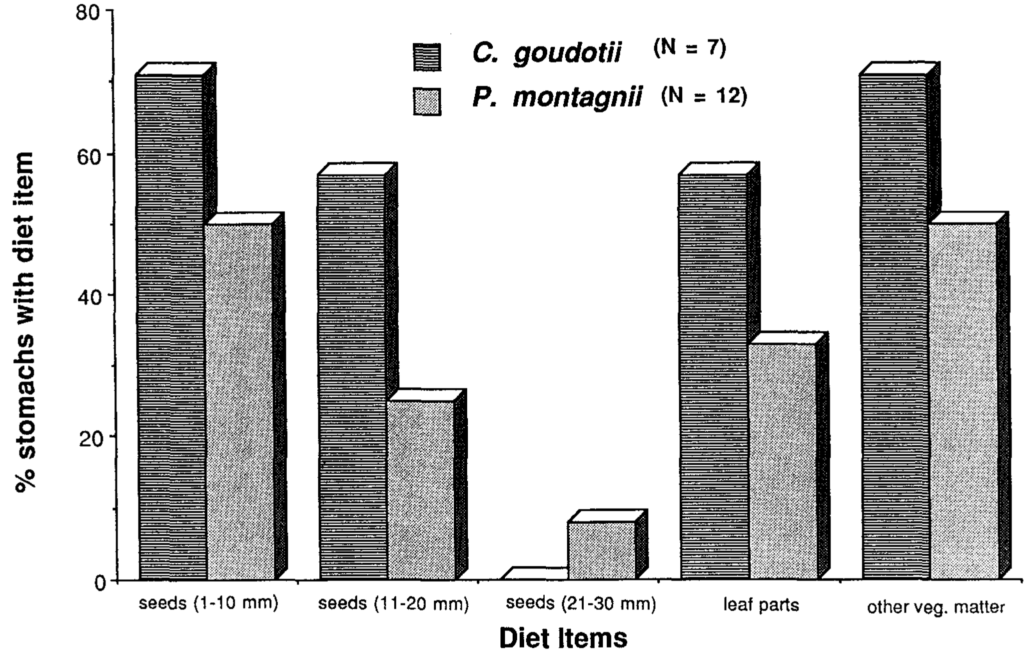

FIGURE 6. Representation of diet items in crops and stomachs of specimens of *Chamaepetes goudotii* and *Penelope montagnii*. The seeds were presumably enclosed by fruit parts, which appeared to form the bulk of the "other vegetable matter."

ural history. It challenges our imaginations to concoct a situation with a firm basis in natural history that proposes that species A outcompetes B at high elevations in one portion of the range, but B outcompetes A at these same elevations in the other portion, with the *reverse* situation at low elevations. Why would *C. goudotii* be able to outcompete *P. montagnii* at high elevations in the southern Andes but the situation be completely reversed in essentially contiguous habitat north of about 11°S? If *P. montagnii* excludes *C. goudotii* from upper elevations throughout most of the Andes, why is it not able currently to exclude it from such elevations in southern Peru and Bolivia?

One solution to the dilemma posed by the guan niche shifts is to challenge the unstated assumption that the system is in equilibrium. As articulated by Wiens (1984), recent thinking concerning community patterns and processes is based too often on assumptions of equilibrium. Certainly, if we change our outlook in the Andean guan situation to one of disequilibrium, then previous objections to all three hypotheses can be countered in part. Perhaps we can view the high-elevation populations of *C. goudotii* in northern Bolivia and southern Peru as the vestige of a time before the appearance of *P. montagnii,* when *C. goudotii* was the only guan through most of its range; this high-elevation, relictual population of *C. goudotii* may be in the process of being eliminated by the expansion of *P. montagnii.* Such a hypothesis can be supported only by gathering evidence on historical changes in the distribution of the two putative competitors or by genetic data that show which taxon is the oldest.

Although we favor the interspecific competition hypothesis, especially with a post-hoc boost from the nonequilibrium hypothesis articulated above, we emphasize that we are uneasy with such an interpretation because the tests mustered in its support are weak. We realize, however, that such uneasiness is probably inevitable given the nature of such "natural experiments" that are not amenable to direct experimentation (but see Diamond [1986b] for the advantages of natural experiments). We also realize that our conclusions are influenced greatly by interpretation. For example, the evidence for competition is weak or open to interpretation: (1) the dietary data, which address only the size of food, are not sufficiently precise to exclude the possibility that major taxonomic differences exist in food items; (2) data on feeding-site selection are nonexistent; and (3) the distributional data show that *C. goudotii* is sympatric with *Penelope* in some areas, particularly outside the Eastern Andes. The importance that one attaches to these points is inevitably based to a degree on one's subjective biases. Data are also nonexistent on nest-site selection, predators, parasites, or diseases. Only by obtaining more refined data that permit stronger tests of the competing hypotheses will the level of analysis be elevated from interpretation to science.

Regardless of the rather unsatisfying results of our attempt to test various hypotheses concerning the underlying processes, we believe that it is important to report this intriguing pattern of distribution of guans of the Andes. Although several examples of elevational niche shifts have been reported in birds of New Guinea and the southwestern Pacific (Diamond 1970, 1972; Diamond and Marshall 1977), we have found only two other cases of elevational niche *reversal* in birds from anywhere else in the world. In the Eastern Andes of northern Colombia and Venezuela and in the Coastal Range of Venezuela, two species of brush-finches (*Atlapetes brunneinucha* and *A. torquatus*) reverse their usual relative position found in the rest of the Andes, where *brunneinucha* is the low-elevation species and *torquatus* the high-elevation species (Schafer and Phelps 1954; Remsen and S. Graves, unpubl. data). A reviewer pointed out to us that Diamond's (1973) map of *Melidectes* honeyeater distribution in New Guinea indicated that two species, *M. ochromelas* and *M. rufocrissalis*, show an elevational niche switch. Also, Andrew Kratter (pers. comm.) has pointed out to us one example of an elevational niche switch in mammals: two species of *Eutamias* chipmunks reverse their relative elevational distributions in the mountains of southern California (Callahan 1977).

Although such anomalies might be regarded as minor because of their rarity, they potentially provide important insights into factors that govern distributional limits. They represent "natural experiments" that may reveal causal factors, or at least provide direction for subsequent research.

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LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed. American Ornithologists' Union, Washington, DC.

BANKS, R. C., AND R. W. DICKERMAN. 1978. Mexican nesting records for the American Bittern. West. Birds 9:130.

CALLAHAN, J. R. 1977. Diagnosis of *Eutamias obscurus* (Rodentia: Sciuridae). J. Mammal. 58:188–201.

CARDIFF, S. W., AND J. V. REMSEN, JR. 1981. Three bird species new to Bolivia. Bull. Br. Ornithol. Club 101:304–305.

CHAPMAN, F. M. 1926. The distribution of bird-life in Ecuador. Bull. Am. Mus. Nat. Hist. 55:1–784.

CONNOR, E. F., AND M. A. BOWERS. 1987. The spatial consequences of interspecific competition. Ann. Zool. Fenn. 24:213–226.

DELACOUR, J., AND D. AMADON. 1973. Curassows and related birds. American Museum of Natural History, New York.

DIAMOND, J. M. 1970. Ecological consequences of island colonization by Southwest Pacific birds. I. Types of niche shifts. Proc. Natl. Acad. Sci. 67: 529–536.

DIAMOND, J. M. 1972. Avifauna of the eastern highlands of New Guinea. Publ. Nuttall Ornithol. Club 12:1–43.

Diamond, J. M. 1973. Distributional ecology of New Guinea birds. Science 179:759–769.

Diamond, J. M. 1986a. Evolution of ecological segregation in the New Guinea montane avifauna, p. 98–125. *In* J. Diamond and T. J. Case [eds.], Community ecology. Harper and Row, New York.

Diamond, J. M. 1986b. Overview: laboratory experiments, field experiments, and natural experiments, p. 3–22. *In* J. Diamond and T. J. Case [eds.], Community ecology. Harper and Row, New York.

Diamond, J. M., and A. G. Marshall. 1977. Niche shifts in New Hebridean birds. Emu 77:61–72.

Dickerman, R. W. 1966. A new subspecies of the Virginia Rail from México. Condor 68:215–216.

Garrett, K., and J. Dunn. 1981. Birds of southern California. Los Angeles Audubon Society, Los Angeles.

Goodwin, D. 1976. Crows of the world. Cornell Univ. Press, Ithaca, NY.

Graves, G. R. 1985. Elevational correlates of speciation and intraspecific geographic variation in plumage in Andean forest birds. Auk 102:556–579.

Haemig, P. D. 1978. Aztec emperor Auitzotl and the Great-tailed Grackle. Biotropica 10:11–17.

Haemig, P. D. 1979. Secret of the Painted Jay. Biotropica 11:81–87.

Holmes, J. A., D. S. Dobkin, and B. A. Wilcox. 1985. Second nesting record and northward advance of the Great-tailed Grackle (*Quiscalus mexicanus*) in Nevada. Great Basin Nat. 45:483–484.

Johnson, T. B., and S. Hilty. 1976. Notes on the Sickle-winged Guan in Colombia. Auk 93:194–195.

Moore, R. T. 1945. The Transverse Volcanic Biotic Province of central Mexico and its relationships to adjacent provinces. Trans. San Diego Soc. Nat. Hist. 10:217–236.

Olrog, C. C. 1960. *Penelope montagnii* en la Argentina (Aves, Galliformes). Neotropica 6:58–59.

Orians, G. 1985. Blackbirds of the Americas. Univ. of Washington Press, Seattle.

Parker, T. A., III, J. V. Remsen, Jr., and J. A. Heindel. 1980. Seven bird species new to Bolivia. Bull. Br. Ornithol. Club 100:160–162.

Parker, T. A., III, T. S. Schulenberg, G. R. Graves, and M. J. Braun. 1985. The avifauna of the Huancabamba region, northern Peru, p. 169–197. *In* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. S. Buckley [eds.], Neotropical ornithology. Ornithol. Monogr. No. 36. American Ornithologists' Union, Washington, DC.

Paynter, R. A., Jr. 1982. Ornithological gazetteer of Venezuela. Museum of Comparative Zoology, Cambridge, MA.

Paynter, R. A., Jr., and M. A. Traylor, Jr. 1977. Ornithological gazetteer of Ecuador. Museum of Comparative Zoology, Cambridge, MA.

Paynter, R. A., Jr., and M. A. Traylor, Jr. 1981. Ornithological gazetteer of Colombia. Museum of Comparative Zoology, Cambridge, MA.

Paynter, R. A., Jr., M. A. Traylor, Jr., and B. Winter. 1975. Ornithological gazetteer of Bolivia. Museum of Comparative Zoology, Cambridge, MA.

Phillips, A. R. 1986. The known birds of North and Middle America. Published by the author, Denver, CO.

Pratt, H. D., B. Ortego, and H. D. Guillory. 1977. Spread of the Great-tailed Grackle in southwestern Louisiana. Wilson Bull. 89:483–485.

Remsen, J. V., Jr. 1985. Community organization and ecology of birds of high elevation humid cloud forest of the Bolivian Andes, p. 733–756. *In* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. S. Buckley [eds.], Neotropical ornithology. Ornithol. Monogr. No. 36. American Ornithologists' Union, Washington, DC.

Remsen, J. V., Jr., and M. A. Traylor, Jr. 1983. Additions to the avifauna of Bolivia, Part 2. Condor 85:95–98.

Ripley, S. D. 1977. Rails of the world. David R. Godine, Boston, MA.

Schafer, E., and W. H. Phelps. 1954. Aves de Rancho Grande. Bol. Soc. Venez. Cienc. Nat. 16:3–167.

Schulenberg, T. S., and J. V. Remsen, Jr. 1982. Eleven bird species new to Bolivia. Bull. Br. Ornithol. Club 102:52–57.

Stephens, L., and M. A. Traylor, Jr. 1983. Ornithological gazetteer of Peru. Museum of Comparative Zoology, Cambridge, MA.

Terborgh, J., and J. S. Weske. 1975. The role of competition in the distribution of Andean birds. Ecology 56:562–576.

Todd, W.E.C., and M. A. Carriker, Jr. 1922. The birds of the Santa Marta Region of Colombia: a study in altitudinal distribution. Ann. Carnegie Mus. 14:1–611.

Vaurie, C. 1967. Systematic notes on the bird family Cracidae. No. 6. Reviews of nine species of *Penelope*. Am. Mus. Novit. 2299.

Vaurie, C. 1968. Taxonomy of the Cracidae. Bull. Am. Mus. Nat. Hist. 138:213–214.

Vuilleumier, F. 1965. Relationships and evolution within the Cracidae (Aves, Galliformes). Bull. Mus. Comp. Zool. 134:1–27.

Wiens, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes, p. 439–457. *In* D. A. Strong, [eds.], Ecological communities. Conceptual issues and the evidence. Princeton Univ. Press, Princeton, NJ.

Williams, M. D. 1980. First description of the eggs of the White-winged Guan, *Penelope albipennis*, with notes on its nest. Auk 97:889–892.

Williams, S. O., III. 1989. Notes on the rail *Rallus longirostris tenuirostris* in the highlands of central Mexico. Wilson Bull. 101:117–120.