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Notes on Nighthawks of the Genus Chordeiles in Southern Middle America, with a Description of a New Race of Chordeiles minor Breeding in Panamá

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According to the American Ornithologists' Union "Check-list of North American birds" (1957, p. 293), the Common Nighthawk, Chordeiles minor, breeds only as far south as Chiapas, Mexico, winters in South America, and occurs in Central America and Panamá only as a transient. A breeding population is here recorded from Panamá, almost a thousand miles southeast of Mexico, belonging to an undescribed subspecies. In a comparison of specimens, local color parallelism was noted with sympatric populations of the Lesser Nighthawk, C. acutipennis. The taxonomic and distributional status of both species in southern Middle America is discussed.

In my study of this group, Oberholser's (1914) monograph proved of basic usefulness, supplemented by Selander's (1954) paper on the western races of *C. minor*. The large collection of the American Museum of Natural History, plus additional examples lent by the Carnegie Museum, the Museum of Vertebrate Zoology, the University of Michigan Museum of Zoology, the Dickey Collection, and the United States National Museum, enabled me to reach certain conclusions regarding this controversial group.

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PREVIOUS INFORMATION REGARDING POSSIBLE BREEDING OF CHORDEILES MINOR IN PANAMÁ

Chordeiles minor has not been considered a breeding species south of Mexico. All Panamá specimens had been taken in April and May or from September to October and identified as northern migrants (Griscom, 1935). Chordeiles acutipennis, though reported to breed from southwestern United States and spottily to Nicaragua and through much of South America, has never been proved to breed in Panamá or Costa Rica; specimens recorded have been considered migrants or winter visitants (Griscom, 1935; Carriker, 1910). Some years ago (1951, p. 184) I remarked on the daily presence about Panamá City, during June and July over several years, of nighthawks that seemed to be C. minor on the basis of appearance, manner of flight, and constant utterance of the familiar penetrating call. In subsequent years I repeatedly observed similarly vocal nighthawks during June and July in the same and other localities along the Pacific slope of Panamá, but I was unable to obtain specimens. The generally silent, low-flying C. acutipennis was also noted during June and July at several localities, usually in drier, less grassy, habitats; specimens were taken by several collectors.

In 1960 two items suggestive of probable breeding came to my attention. On June 14, at Cerro Campana, in the western part of Panamá Province, Richard Ryan and Ned Boyajian flushed a dark nighthawk, which did the "broken-wing" display. Although they could not vouch for the specific identity of the displaying bird, all nighthawks they saw flying that evening called like C. minor—which had been my own experience on prior visits to the same locality. L. I. Davis informed me (and briefly reported in Audubon Field Notes) that while in Panamá in 1960 he had taken tape recordings of C. minor booming, as well as calling, on April 10, at Cerro Azul, east of Panamá City, and that on April 20–21 in savanna country east of Natá, Coclé, he had also heard booming by C. minor and trilling and whinnying by C. acutipennis, behavior he regarded as territorial and evidence of breeding. Such a conclusion seemed reasonable, but in April northbound transients might display.

If there was a Panamá breeding population of *C. minor*, it seemed likely that, being so distant from any other known breeding population, recognizably distinct morphological characters would appear. I therefore checked the examples of *C. minor* recorded in the literature as taken in Panamá and Costa Rica. To supplement the collection in the American Museum, specimens were borrowed, including the topotypical series from Chiapas of the recently described *C. m. neotropicalis* (Selander and Alvarez del Toro, 1955). The American Museum had two adult *C. minor* taken in

May on the Pacific slope of the Canal Zone, near Panamá City. The collector, Hallinan, had reported (1924, p. 315) as to the female (flushed at the edge of a mangrove swamp near Balboa, on May 13, 1913) that "one egg was well developed in the ovaries." The adult male had been taken "out of a small flock on the wing" on May 21 at Corozal. Griscom (1935), in his Panamá check list, treated these birds as migrants of the northern race, C. m. minor. (A January nighthawk listed in Hallinan's paper as C. minor proved to belong to the other species, C. acutipennis.) Two other specimens, from Chiriqui Province in extreme western Panamá. taken October 24 and November 4, 1905, seemed to be immature. These four Panamá examples, as well as a July adult female from Hacienda El Pelón, Guanacaste, Costa Rica (Dickey Collection), were alike and differed from other populations in combining small size, dark rufescent color, and markedly reduced white band on the primaries. In general pattern they resembled less the Chiapas form, neotropicalis, than the more distant Florida race, chapmani, which is essentially like the northeastern minor but for smaller size and slightly paler color. The reduced wing spot, which in both adult females and immatures was restricted on the outermost pair of primaries to the inner web (failing to reach the shaft by from 3 to 5 mm.), seemed a distinctive feature. With so few examples, some doubt remained as to the existence of a Panamá breeding population, because an occasional juvenal female of chapmani (and very rarely of minor) may have the wing spot miss the shaft by between 2 and 4 mm., and even more rarely may have the spot obsolescent. Moreover, as Selander (1954, p. 62) first noted, at least some individuals retain juvenal primaries through the spring and summer following the year of hatching.

PROOF OF BREEDING IN PANAMÁ

On April 9, 1961, and repeatedly thereafter, I saw and heard Chordeiles minor calling over Paitilla Airfield, at sea level in Panamá City. On April 30 James E. Ambrose and I noted several C. minor calling near the larger Tocumen Airport, some 20 miles east of Panamá City. On May 6, Ambrose accompanied me to Cerro Campana, where we had both observed C. minor in previous years and where searching for a breeding bird seemed more practical than on active airfields. Cerro Campana is a volcanic ridge, rising to about 3000 feet in western Panamá Province, roughly 30 miles southwest of the Canal Zone, overlooking the Pacific Ocean (Panamá Bay). The southern and western slopes are open, having scanty vegetation of grass, sedge, and low bushes, interspersed with "islands" of low, dry woodland. The upper elevations are cool and windy and often have fog. The northeastern slopes support (or did support until

recent clearing) considerable areas of humid forest, with a distinct tinge of "cloud forest" (subtropical) avifauna. On May 6 the rainy season was just beginning; new grass and sedge were sprouting, and we encountered some drizzles. That night at about 6.30 p.m., we heard two, possibly as many as four, nighthawks giving the characteristic penetrating, nasal "bzheent," or "bzheep." The next afternoon Ambrose, by chance, flushed a female from a downy chick on an open rocky hillside. The female flew to a tree at the edge of a nearby patch of dry woods and watched us as we examined the chick. The chick rested on bare stony ground with some shell fragments. A little grass and a bush grew a few feet away. The chick was covered with down; its eyes were open; no feather papillae showed. It called a plaintive "pee-oo" constantly, but did not move when touched. I doubt that its age could have exceeded two or three days (cf. Gross in Bent, 1940, p. 221). When the female returned to cover the young, both birds were collected.

CHARACTERS OF THE NEW RACE

The female shows the characters previously noted in the birds taken by Hallinan and confirms the existence of a distinct breeding population in Panamá.

Chordeiles minor panamensis, new subspecies

Type: Adult female, A.M.N.H. No. 768852, taken at Cerro Campana, Panamá Province, Panamá, at about 2500 feet, on May 7, 1961, by James E. Ambrose, Jr. Wing (chord), 180; tail, 95; left ovary, 8 mm. Iris dark. Wing measurement taken to tip of ninth primary, as outermost (tenth) broken. [Measurements taken to tenth primary are usually slightly longer (ranging from about the same to 3 mm. more) than those taken to ninth.] Collected while brooding one downy nestling.

DIAGNOSIS: Resembling C. m. chapmani of Florida in blackish dorsal color, in relatively broad blackish ventral barring, and in small size, but differing in having white wing band markedly reduced, in generally darker and much more rufescent tone, being speckled and mottled dorsally with deeper tawny and rufous, and having the ventral ground color deeper buff in males and tawny in females, and, probably, in relatively shorter tail. Speckling on blackish pileum, hind neck, scapulars, lesser wing coverts and fore neck is rufous (Orange-Rufous to Sanford's Brown of Ridgway) rather than buff; mottling on the middle and greater wing coverts and "tertials" is chiefly buff or rufous, rather than chiefly whitish or buffy gray; ground color of breast, abdomen, and under tail coverts

tawny (Cinnamon-Buff to Ochraceous-Tawny) in females, and deep buff fading to cream buff in the one adult male, rather than buff in females and whitish to cream buff in males. White wing patch reduced on outermost (tenth) primaries: in adult females confined to inner web and very narrow (6–9 mm. at widest part), narrowing to an oval tip (sometimes almost a point) as it approaches shaft, but not reaching shaft (missing shaft by 3–5 mm. in specimens examined; by 4 mm. in type); in the one adult male, wing band on outermost primary not extending to outer web but reaching shaft, narrowing there to width of 8–9 mm. from maximum width of 12 mm. at edge of inner web.

Compared with C. m. neotropicalis of Chiapas, panamensis differs, sex for sex, in darker, more rufescent, color, in reduced wing band (in adults examined of neotropicalis maximum width on tenth primary: males, 14–16 mm.; females, 10–11 mm; in both sexes reaching shaft); in broader black ventral barring, almost as wide as light interspaces; in deeper, but less coarse, rufous mottling above; and deeper tawny color below. The one adult male panamensis, unlike the neotropicalis males, has the white tail band extending across both webs of the outer rectrices and is wider (10 mm. wide at middle of inner web, 12 mm. at shaft, 5–6 mm. on outer web).

In the blacker, less coarsely mottled, dorsal surface, and in the broader, blackish, ventral barring, *panamensis* is similar to *chapmani* and to nominate *minor* and differs from all other described races.

Downy Chick: Above sooty black, mottled throughout with rufescent fawn; below rufescent fawn, with some sooty black on the fore neck and sides. (Specimen preserved as a mummy after injection with formalin.) Compared with a very young downy chick of C. m. chapmani from Wilsonville, Alabama, in the United States National Museum, and an older downy of C. m. minor from New Brunswick, Canada, the dark areas in panamensis are blacker, and the light areas are strongly rufescent, rather than light gray. Gross (in Bent, 1940, p. 221) describes the downy of nominate minor as having the mottling and ventral surface "pallid neutral gray" and the dark areas "dark mouse gray." Apparently the distinctive combination of dark color and rufescence, characteristic of panamensis, appears at the earliest stage.

Measurements: Panamá: Adult male: Corozal, Canal Zone, wing, 187; tail, 99. Immature male: Frances, Chiriquí: wing, 175 (worn); tail, 95. Adult females: Cerro Campana, Panamá (type), wing, 180 (tip of ninth primary); tail, 96; Balboa, Canal Zone, wing, 175; tail, 97; Chepo, Panamá, wing, 184; tail, 97. Immature female: Frances, Chiriquí, wing, 172 (worn); tail, 96. Costa Rica: Adult female: Hacienda El Pelón, Guanacaste, wing, 185; tail, 96.

TABLE 1				
Comparative Measurements ^a (in Millimeters, with Averages in Parentheses) of				
CERTAIN SUBSPECIES OF Chordeiles minor				

	panamensis	neotropicalis (Chiapas only)	chapmani (Florida only)
Adult males			, ,
No.	1	6	10
Wing	187	188-199 (195.3)	178-192 (184.1)
Tail	99	103-112 (106.8)	99–110.5 (105)
Adult females			, ,
No.	4	2	10
Wing	175-185 (181 ^b)	178-187 (182.5)	172.5-184.5 (179.4)
Tail	96–97 (96.5)	95–96 (95.5)	99–108.5 (103.2)

^a Measurements for *chapmani* were taken from Oberholser (1914, p. 75); those for male *neotropicalis*, from Selander and Alvarez del Toro (1955, p. 146); those of the two females of *neotropicalis* were taken by me. My measurements of nine adult females of *chapmani* from Florida are close to Oberholser's: wing, 176–189 (181.8); tail, 96–108 (104.2).

RANGE: Pacific slope of Panamá in open grassland from western Chiriquí to eastern part of Panamá Province; also on Pacific slope of northwestern Costa Rica.

Specimens Examined: Chordeiles minor panamensis, eight: Panamá: Corozal, Canal Zone, one adult male; Frances, Chiriquí, one immature male; Cerro Campana, Panamá, one adult female (type); Chepo, Panamá, one adult female (U.S.N.M.); Balboa, Canal Zone, one adult female; Frances, Chiriquí, one immature female; Cerro Campana, Panama, one downy chick, unsexed. Costa Rica: Hacienda El Pelón, Guanacaste, one adult female "[9]o" " (U.C.L.A.). Chordeiles minor neotropicalis, 10: Mexico: near Ocozocoautla, Chiapas, five adult males, two adult females (all M.V.Z.). Chordeiles minor neotropicalis

aserriensis, three: Mexico: Tampico, Tamaulipas, one adult male, one female; Veracruz, one adult male. Chordeiles minor aserriensis, 31: Costa Rica: San José, one immature male (type). Texas: Tivoli, eight adult males, seven immature males, 10 adult females, five immature females. Chordeiles minor chapmani, 46: Florida, 23 adult males, two immature males, 12 adult females, six immature females (one, U.S.N.M.). Alabama, one downy (U.S.N.M.). Arkansas, one immature female (U.S.N.M.). Georgia, one juvenal female (U.S.N.M.). Chordeiles minor minor, 50: Eastern United States, 10 adult males, five immature males, 10 adult females, five imma-

^bThe average length of wing for *panamensis* includes the type with broken tenth primaries. The average wing length might have been increased by about 1 mm. had measurement of this example been possible to the tenth primary.

ture females. Western Canada: Okanagan, British Columbia, 10 adult males, 10 adult females. Chordeiles minor henryi, 18: Southern Arizona, three adult males, four adult females. Southern New Mexico, one adult female. Western Texas, five adult males, two adult females. Chihuahua, Mexico, one adult male, two adult females. Chordeiles minor howelli, 14: Northern New Mexico, one adult male. Wyoming, one adult male. Utah, four adult males, two females. Colorado, three adult males, one immature male, two adult females. Chordeiles minor sennetti, eight: Kansas, three adult males, two immature males, one adult female, two immature females. South Dakota, one immature male. Chordeiles minor hesperis, 12: California, eight adult males, four adult females. Chordeiles gundlachii gundlachii, 14: Greater Antilles, eight adult males (including the type), five adult females (three, U.S.N.M.), one immature. Chordeiles gundlachii vicinus, 10: Bahamas, five adult males, four adult females, one downy (all but two, U.S.N.M.).

All the specimens that are mentioned, unless otherwise indicated, are in the American Museum of Natural History collection. That collection includes many additional specimens of the northern subspecies, which, though examined, are not listed, because they were either cumulative or may represent migrants of questionable value in the determination of subspecific characters. I have seen two Panamá examples, in the Museum of Comparative Zoölogy, taken on the Caribbean coast on October 15 and 18, 1928, allocated by Griscom (1932, p. 72) to nominate minor and to sennetti. While my examination was insufficient for subspecific allocation, these birds were clearly northern migrants, not panamensis.

Remarks: The female from Chepo, eastern Panamá Province, taken by Wetmore and Perrygo, on April 21, 1949, in the United States National Museum, is not quite so deeply tawny below as the other females, and the light ventral interspaces seem a bit wider, thus perhaps showing some approach towards neotropicalis. The Costa Rican example from Hacienda El Pelón, Guanacaste (700 feet, 15 miles north of Liberia), taken on July 27, 1928, by Austin Smith, shows the characters of the darkest Panamá females, having even more rufous speckling above, and a very reduced wing band. It is labeled "[$\mathfrak{P} \supset \mathfrak{F}$," and appears to be an adult female; the original sexing as a male may have been based on the rather whitish throat.

Not listed above are two other Costa Rican specimens that on the basis of date suggest breeding birds, but seem too large for *panamensis*, unless missexed. These examples, labeled as females (Carriker Collection, Carnegie Museum), taken at Miravalles, Guanacaste, are dated May 25 and June 27, 1906. Oberholser, in his review of the genus (1914, p. 77),

expressed the view that the June date must be an error for May, because C. minor did not breed in Central America and the dates given in Carriker's paper (1910, p. 501) were May 24 and 25. Oberholser identified the "June" bird as chapmani and the somewhat larger May 25 example as virginianus (= nominate minor). The collector's numbers on the labels (2587) and 2876) are consistent with the specimens' having been taken a month apart, and Carriker's paper (1910, pp. 366, 910) indicates that collecting was done in Miravalles in late June as well as May. In view of Carriker's general comment that no nighthawks breed in Costa Rica, it is surprising that he did not refer specifically to the collection of these remarkably late birds. Possibly they were taken by Lankester, who collected birds for Carriker in Guanacaste. Both Miravalles examples agree with panamensis in having a small wing patch (not reaching within 3 mm. of the shaft), dark dorsal surface, broad ventral banding, and tawny under parts, but for females of panamensis they seem too large (wing, 194, 191; tail, 101, 100). They are also slightly less rufescent above than Panamá birds, and the larger individual is somewhat more coarsely mottled. If these were actually missexed year-old males, retaining juvenal primaries, I would attribute them to the new form. Three other C. minor taken by Carriker on September 24-26, 1904, "from a large flock on the Caribbean coast," at Rio Sicsola (now the Costa Rica-Panamá boundary) are certainly transients. Oberholser assigned two to "virginianus" [now nominate minor] and a smaller female (wing, 188; tail, 101) to chapmani. I would allocate the last-mentioned bird also to minor, as the smaller size is consistent with its age, for it has juvenal primaries (see Selander, 1954, pp. 64-65).

Chordeiles virginianus aserriensis Cherrie (1896, p. 136) was described from a single Costa Rican male, taken near San José on November 2, 1893. The location of the type has been regarded as unknown (Friedmann, Griscom, and Moore, 1950, p. 152). It is now in the American Museum (ex Rothschild Collection). Oberholser (1914, pp. 71-74), though unable to locate the type, concluded from the description that the bird was not an adult and applied the name to the then undescribed smallish population of southern Texas. As Oberholser surmised, the type is a bird passing from juvenal to first autumn dress, and certainly it is an example of one of the palest northern populations, representing the opposite color extreme from panamensis. Dorsally it is of a gray and whitish tone and ventrally very white, the black barring being extremely narrow, almost wholly absent from the under tail coverts. The resemblance is close to juvenals of the Great Plains sennetti, but as some immature examples from south Texas seem indistinguishable from sennetti except for size, and as Cherrie's bird is small (wing, 177; tail, 103), it is reasonable to preserve

the nomenclatural allocation made by Oberholser.

Examples of *C. minor* from Veracruz, Veracruz (June 15, 1957), and Tampico, Tamaulipas (July 14, 1958), collected by Selander, seem to me to be intergrades between *neotropicalis* and *aserriensis*; they are lighter and grayer than Chiapas specimens and darker than the south Texas population. The female from Tampico (wing, 183; tail, 99), while otherwise quite unlike that of *panamensis*, has the wing band more reduced than the two Chiapas females, not reaching the shaft by 3.5 mm.; it is probably a year-old individual with juvenal primaries.

Chordeiles minor henryi, though very rufescent, is readily distinguished from panamensis. It is a large race, with broad wing band, and, like the other western subspecies, has narrow ventral barring and coarse dorsal mottling. A specimen taken in June in Colombia attributed to henryi (de Schauensee, 1949, p. 509) should be reëxamined.

Chordeiles gundlachii: The small West Indian nighthawks are usually divided into two races, gundlachii of the Greater Antilles and vicinus of the Bahamas. Bond (1956, p. 88) does not consider the latter worthy of recognition; he regards it simply as a gray phase of gundlachii that also occurs in the Greater Antilles. I have examined too few specimens to have an opinion on this point. Unlike the continental races of C. minor, but like some populations of C. acutipennis, the Antillean population shows very distinct gray and ochraceous phases. In any phase the birds are smaller than banamensis, lighter and more mottled above, with narrower black bars below. All West Indian, breeding-season adults examined (including those from the Bahamas) have the lower abdomen and under tail coverts buff or ochraceous, somewhat contrasting with the color of the breast, which is grayish, usually vermiculated or speckled (rather than distinctly barred) with blackish, thus presenting a pattern more usual in C. acutipennis than in C. minor. The West Indian adults have wider wing bands than panamensis of corresponding sex, though in a few adult females of gundlachii and Bahamian vicinus the band fails (by 1-2 mm.) to reach the shaft of the outer primaries. One full-grown immature female (gray phase) taken in June, 1863, at Spanishtown, Jamaica, is remarkable in having the wing spot obsolescent, being completely absent from the outermost (tenth) primaries. (This condition is very rarely approached by immatures of chapmani.)

It has been frequently noted that the call of the West Indian Nighthawk (in the Bahamas as well as in the Antilles) is quite unlike that of the continental races of *C. minor*. The call has been verbalized as a katydid-like "chitty chit chitty chit" (Wetmore and Swales, 1930, pp. 255–257) and as "pity-pit-pit" (Bond, 1960, pp. 259–260); its three- or four-note

character is indicated by its various local names (Bond). McCandless (1958, p. 34) mentions also "a short weak 'burr.' " All observers agree that the West Indian birds do not utter any note like the penetrating nasal "peernt" (or "bzheeent") characteristic of C. minor. According to Wetmore, the diving display of the male ends with a rather weak, higherpitched whirring, less resonant than the roaring boom of C. minor. In wing pattern gundlachii (including vicinus) resembles C. minor, and gray-phase birds suggest a small subspecies of the latter. Some years ago West Indian nighthawks were collected breeding on the southern Florida Keys and assigned to vicinus (American Ornithologists' Union, 1957, p. 296). On the mainland of southern Florida C. minor chapmani (which calls like other races of C. minor) is a common breeder. For some time the two forms have been almost, if not actually, sympatric. In June and July, 1961, Alexander Sprunt, IV, found, in a recently cleared area of southern Key Largo, Florida, two nests about 300-400 yards apart, which he identified as belonging one to one form and one to the other, on the basis of the distinctive calls of the males guarding the incubating females (oral communication). During the same summer, in northern Key Largo, Henry M. Stevenson heard both types of calls (in litt.), and collected C. minor chapmani. Years ago Wetmore (Wetmore and Swales, 1931) expressed the opinion that C. gundlachii was specifically distinct from C. minor, and the latest check list of the American Ornithologists' Union (1957, p. 296) suggested in a footnote that such might prove to be the case. Aside from the recent observational evidence of actual sympatry, the circumstance that the distant banamensis calls like all other races of C. minor, while the nearby gundlachii does not, is additional evidence of specific distinctness. In crepuscular and nocturnal birds striking vocal differences between contiguous populations are indicative of reproductive isolation (possibly of character reënforcement), even though plumage differences suggest a conspecific relationship.

DISTRIBUTION OF CHORDEILES IN PANAMÁ AND SOUTHERN CENTRAL AMERICA

STATUS OF Chordeiles minor

As mentioned above, proof of breeding by C. minor has not hitherto existed in Middle America south of Chiapas, Mexico.

Panamá: Although specimens are few, C. minor apparently breeds widely in the open grassland on the Pacific slope of Panamá from near the Costa Rica border in Chiriquí at least to east of Panamá City, as indicated by the following observations.

During the years 1948-1956 inclusive (except 1954), I spent mid-June to mid-July in Panamá in a suburb of Panamá City east of the Canal Zone. Every evening I heard and saw C. minor flying over or near the house above the adjacent open grassland; usually the birds appeared at about 6.00 P.M. and continued calling to about 7.00 P.M. Sometimes I heard them just before sunrise. I did not hear or see nighthawks at this locality (now rather built up) in April-May, 1961, but I found them regularly less than a mile away, over Punta Paitilla Airfield from April 9 to May 16, when I left Panamá. They almost surely breed there and also at or near Tocumen Airport, farther east, and very likely throughout the Panamá savannas. West of Panamá City I had previously encountered calling C. minor at Cerro Campana, the proved breeding site, on July 10, 1955, and June 24-26, 1956, and at several places farther west: in Coclé Province (El Valle de Antón, about 2000 feet, July 6, 1952); and in Chiriquí Province (El Hato, about 4200 feet, August 1, 1945; below Bambito near Llanos del Volcán, about 5000 feet, July 9, 1948).

Further indicative of an almost continuous range along the open Pacific slope of Panamá are the observations, mentioned above, by L. I. Davis of booming in April, at Cerro Azul, Panamá Province, and near Natá, western Coclé. I also have a report from Robert Scholes of "about a dozen" calling over Ocú, Herrera, on May 27, 1951.

I have failed to note *C. minor* in one open section of the Pacific slopes where it might be expected, namely, the badly eroded and rather sterile Llanos de Coclé district of southeastern Coclé and the adjacent western part of Panamá Province, where in June and July I have repeatedly found the Lesser Nighthawk, *C. acutipennis*. On the more humid Caribbean slope, even in cleared areas, *C. minor* seems to be absent, except during migration, when large numbers of silent, high-flying nighthawks have been observed in autumn (September and October). These birds are doubtless transients of northern populations.

From December to March inclusive, so far as I am aware, no specimens of C. minor have been taken in Panamá (or anywhere in Central America). In 1960 I spent late January to early March in Panamá without seeing this species. I have never heard one in Panamá later than the first week of August, although specimens have been taken there into November. Alexander Wetmore, who has collected in Panamá over many years from January to April, writes me that his earliest observations of C. minor are of birds calling on March 24 and 29 and April 1, 1949, near the La Jagua Gun Club in the savanna beyond Pacora, east of Panamá City. Probably C. minor panamensis "winters" in South America, as do other populations of the species, which should not be surprising, for the northern

winter is contemporaneous with the dry season of the northern tropics, when the Pacific grasslands become parched and high-flying insects very scarce. I visited Panamá in August, 1954, and September, 1958, and on each occasion saw only a single silent nighthawk in the Panamá City area where the birds are vocal and common in June and July. As the dry season does not begin until December, an early exodus of the local population is suggested. The possibility remains, however, that the nighthawks merely leave their usual haunts without actually emigrating and are overlooked because they are silent. However, the Lesser Nighthawk, though usually silent, can be observed (and has frequently been collected) in suitable areas of Panamá throughout the year.

CENTRAL AMERICA: Some evidence of a Central American breeding population of C. minor is the collection of three specimens in Costa Rica at a period when northern birds would not be expected. Two of these specimens (those mentioned above from Miravalles), if correctly sexed, may be stragglers. But one, the July 27 adult female from Hacienda El Pelón, Guanacaste (Dickey Collection), is so unlike northern birds and shows in such accentuated degree the characters of the Panamá breeding population that it must represent the same race. Hacienda El Pelón is in the northwestern corner of Costa Rica, near Nicaragua; the avifaunal affinities of the area are with Central America rather than with Panamá. There is no reason to suppose that in a northern species like C. minor a real gap in breeding range exists between Chiapas and Panamá. It should be noted that Paul Slud observed no nighthawks at Hacienda El Pelón during a stay from May 26 to 30, 1961, but he advises me that this finca is enormous and nighthawks may have been present in a section not visited. Moreover, as nighthawks wander about after the breeding season, a late July specimen might have bred elsewhere, though probably at no great distance.

L. I. Davis has recently informed me that in 1961 he heard nighthawks booming in British Honduras, which strongly suggests breeding by this species. Though British Honduras is north of Chiapas, it is an area from which *C. minor* has not been reported to breed.

STATUS OF Chordeiles acutipennis

The Lesser Nighthawk, though essentially a tropical species, has a somewhat uncertain status in Central America. Oberholser (1914, p. 91) considered that it bred from southwestern United States to Guatemala and British Honduras and widely in South America to southeastern Brazil, but he had no summer records between Honduras and Panamá

inclusive. Such experienced field workers as van Rossem in El Salvador (Dickey and van Rossem, 1938; see also Rand and Traylor, 1954), Carriker in Costa Rica (1910), and Griscom in Panamá (1938) considered that this species was simply a transient and winter resident. Friedmann, Griscom, and Moore (1950) gave the breeding range of *C. a. micromeris* as extending to Nicaragua, based on a specimen mentioned below. I now feel sure it will prove to breed in suitable localities throughout Middle America, though I indicated uncertainty in my Middle American list (1955).

There are many more specimens of *C. acutipennis* than of *C. minor* from southern Central America and Panamá, presumably because northern migrants of *C. acutipennis* winter in the area, while those of *minor* are merely transients. The presence of northern birds for much of the year, combined with the color variability of this species, has made it difficult to recognize local populations. We need specimens proved to be breeding, or, failing that, examples taken when migrants would presumably be absent (late May to July).

Panamá: I am not aware of any proved breeding specimen. A number of specimens have been collected in June and July. Even in tropical Mexico, where the breeding season is probably earlier than farther north, many birds must still be engaged in reproductive activities into July (see Paynter, 1955, p. 138). While some individuals may migrate earlier, there is therefore reason to believe that Lesser Nighthawks taken in Panamá in June and early July are probably a local population. Strong corroboration exists in the fact that specimens taken during this period are readily distinguishable from all Mexican and United States populations, averaging smaller and being much darker and ruddier, and barred (rather than streaked) on the back. In fact in their dark and ruddy color they parallel the local race of *C. minor*.

On successive evenings, June 20–23, 1953, Alexander Wetmore and I observed over the highway near San Carlos, in the scrubby western part of Panamá Province, on the Pacific slope between Playa Coronado and Río Mar, a loose flock of from a dozen to 50 of these nighthawks. On June 21 Wetmore collected in the area a grayish male just molting out of juvenal plumage. On June 22 he collected from the flock three adults (two males and one female), all dark, small, ruddy individuals. A female (preserved in formalin) was taken in the suburbs of Panamá City on June 29, 1953, by Richard Bennett. All these specimens are in the United States National Museum. J. A. Weber collected on July 26, 1928, at Fort Davis, Caribbean slope of the Canal Zone (and definitely not a breeding site), a female (wing, 157; tail, 87), very small, dark, and ruddy, which the late W. de

W. Miller and J. T. Zimmer both identified as the nominate South American race, C. a. acutipennis. These Panamá birds represent a breeding population closest to the South American acutipennis among currently described subspecies and are quite distinct from micromeris or any other Mexican race.

The main Panamá breeding area for this species is probably the rather arid, scantily vegetated Pacific lowlands of Coclé. During June and July I have repeatedly seen individuals or flocks of these low-flying, silent birds in Coclé, over sandy areas about Río Hato Airfield and in the strongly eroded badlands near the road to El Valle. Less often I have noted individuals or flocks in the adjacent, more scrubby, country of western Panamá Province. L. I. Davis' report of a bird trilling and whinnying on April 21, 1960, near Natá, Coclé, probably represented, as he interpreted it, territorial behavior on the breeding grounds. As with the other species, the main breeding period is probably April and May. The birds taken by Wetmore in late June had evidently finished breeding.

COSTA RICA: Three females taken at Hacienda El Pelón, Guanacaste, by A. Smith on July 30 and August 1, 1928, are mentioned by Dickey and van Rossem (1938, p. 245; wing measurements given as 158, 165, 162 mm.). These measurements would fit either micromeris or the smaller nominate acutipennis. The largest individual (University of California at Los Angeles, Dickey Collection, No. 22694) taken July 30, was lent to me. It is an extremely dark and rufescent adult female (wing, 165; tail, 93), definitely much too dark for any Mexican population. I have compared it with the large number of Mexican examples, among them the series of inferior and micromeris (including types), in the United States National Museum and the American Museum of Natural History, and with the topotypical series from Arriaga, Chiapas, of C. a. littoralis Brodkorb (1940, p. 543), lent by the University of Michigan. The specimen agrees reasonably well with nominate acutipennis from Cayenne and northern South America, and even better with the Panamá examples taken in June by Wetmore and with a breeding female from Tipitapa, Nicaragua; it is, however, somewhat blacker and more rufous-speckled dorsally than any of these. In fact, this El Pelón bird appears to be most similar in dorsal pattern and color (though differing in diagnostic wing characters and size) to the C. minor taken at the same locality three days before. The parallelism is so striking that at first glance one might suppose these individuals of two different species were representatives of the same subspecies. Another Costa Rican female, from Río Palo Seco, September 24, 1952 (University of Michigan Museum), appears to belong to the same dark ruddy population, but being an immature bird

in post-juvenal (first basic) plumage (with juvenal primaries), it is smaller (wing, 157; tail, 87) and not quite so dark. Paul Slud, the collector of this example, advised me that Río Palo Seco could not be a breeding site. As already noted in Panamá, nighthawks wander locally after the breeding season.

NICARAGUA: A female from Tipitapa, Managua, taken by Miller, Griscom, and Richardson, April 28, 1917, in the American Museum of Natural History, provides, to my knowledge, the only conclusive breeding record of C. acutibennis from southern Central America. The specimen (wing, 165; tail, 91) is labeled: "Had one downy young a few days old (at most) and one egg ready to hatch." This example is distinctly darker and more rufescent than Brodkorb's series of littoralis from Chiapas or than any example I have seen from farther north, including a few from Guatemala and Honduras (possibly migrants). It has the barred (rather than streaked) back pattern of nominate acutipennis, is as dark as a topotypical series from Cayenne, and, although dorsally not quite so dark, nor so speckled with rufous, as the July 30 female from Costa Rica, it is a shade deeper rufous ventrally. It seems to belong to the same subspecies. Though a new subspecies could be described, based on the dark rufescent birds from Nicaragua to Panamá, it seems best to assign this geographically intermediate population to nominate acutipennis, at least until there is a general revision of the species based on an adequate series of breeding birds. It should be noted that the range given by Oberholser (1914) to nominate acutipennis (type locality, Cayenne), covering almost all of tropical South America as well as southeastern Brazil, includes several undescribed populations that seem as much entitled to recognition as the various northern forms. For example, compared with Cayenne birds, Amazonian adult males (Villa Imperatriz and Río Negro) have the white wing band much broader (18-24 mm. at shaft of tenth primary, instead of 10-18 mm.), those from southeastern Brazil average larger, and there is some indication that those from the humid Pacific slope of Colombia may be darker and ruddier. Miller (1959) has recently separated the ventrally paler population of the less humid upper Magdalena Valley of Colombia.

Comments on the Southern Mexican Populations: Though the series of presumably breeding birds examined by me is small, a few observations on the rather confused Mexican situation may be useful. The breeding populations from Yucatán, southern Mexico, and Central America were described by Oberholser (1914) and named micromeris (type, Xbac, Yucatán), and those from southern Baja California were named inferior. Brodkorb (1940, p. 543) compared breeding examples

from Arriaga, Chiapas, with Yucatán micromeris, found them more mottled with ochraceous, and named a new form, littoralis. Van Rossem (1942, pp. 73–74) concluded that inferior should be merged in micromeris, after comparing examples from Baja California, Sonora, Costa Rica, and El Salvador (those from El Salvador, apparently migrants, having been identified by Oberholser as micromeris). Van Rossem did not mention comparing Yucatán specimens, nor did he comment on littoralis. Wetmore (1943, p. 42) expressed agreement with van Rossem's taxonomic conclusion but dissented from his adoption of the name micromeris.¹ Recently Wetmore has told me that he is now inclined to believe that Baja California and Yucatán birds may be different subspecies.

How many subspecies should be accepted as breeding in Mexico depends on one's philosophy as to the function of nomenclatural recognition. The population of Yucatán is not morphologically the same as that of Baja California, though I would feel no assurance in allocating many migrants captured away from the breeding grounds. The population from Chiapas seems very distinct from that of Baja California, and is also different from most Yucatán examples, though some individuals of each closely approach one another, and there is probably intergradation at the base of the Yucatán Peninsula.

Birds from Baja California (seven males, eight females, and two erroneously sexed as males) give a gray impression dorsally, are lighter above (especially on the crown), and have finer dorsal vermiculations and distinct black dorsal shaft streaks. In pattern they resemble *texensis* but are smaller and average paler. Only one June Cape San Lucas bird (in the United States National Museum), sexed by Xantus as a male but evidently a female, is rather ochraceous above.

The Yucatán micromeris series that I have examined, taken from April (the type) to June (five males and three females), most of which is in the United States National Museum, is distinctly more varied. Some birds (including females) seem as gray above as the Baja California average, though they appear to be more coarsely vermiculated with black on the back and have more black on the crown. Other individuals are much browner-toned (because of buff and ochraceous mottling), closely approaching the duller-colored Chiapas individuals, though perhaps more definitely streaked on the back.

¹ Wetmore, following the American Ornithologists' Union Code of Nomenclature, considered that *inferior* had priority, because of line anteriority over *micromeris* in Oberholser's key, even though the latter had page priority in the formal descriptions. Under the current International Code of Zoological Nomenclature, line and page priority are not controlling, and, if the two subspecies are merged, the choice of name is that of the first reviser—in this case van Rossem.

Adult males of Brodkorb's Chiapas series of *littoralis*, taken in late May at Arriaga (six males, one juvenal female), are not entirely uniform. They certainly are more ochraceous than most Yucatán males and lack (or barely suggest) streaking on the interscapulars, giving a dorsally barred effect more like that of nominate acutipennis. The dullest, least ochraceous, Arriaga individuals are perhaps indistinguishable from the brightest Yucatán males, and these are the ones that have some indication of dorsal streaks. A male and female taken, respectively, at San Bartolomé and Tuxtla Gutierrez, Chiapas, in late May (in the United States National Museum) are like the more ochraceous Arriaga birds, but show slight dorsal streaking. Birds taken in the breeding season in adjacent Guatemala are also similar. A series (three males and three females) from Pie de la Cuesta, Guerrero, August 23–27, 1950 (University of Michigan Museum), agrees well with the Arriaga series, while the adults of a small sample from La Placita, Michoacán (one male, two females, one juvenal), taken July 12-17, 1950 (University of Michigan Museum), seems slightly less ochraceous and more streaked on the back than the dullest Chiapas individuals.

The populations of central Mexico presumably represent intergradation between the larger, duller-colored, more streaked population (texensis) of the more arid north and the smaller, more richly toned population (littoralis) of the more humid south. As the geographically intervening populations are more ochraceous, the similar gray tone of Baja California (inferior) and many Yucatán birds (micromeris) probably reflects convergence resulting from arid climate or similar soil color, rather than an intimate genetic relationship. If micromeris and inferior are lumped in one geographically variable subspecies, then littoralis should not be accorded recognition, but if both races described by Oberholser are accepted, then littoralis can well be admitted.

COLOR PARALLELISM AND ADAPTATION TO SOIL AND CLIMATE

The ochraceous mottling of the Chiapas population of *C. acutipennis* parallels that of the Chiapas population of *C. minor*. The convergence in general appearance and color is not so striking, however, as in the specimens of *C. minor* and *C. acutipennis* taken at Hacienda El Pelón, Costa Rica. Panamá examples of these two species are also very similar in dark and rufescent color and pattern.

Selander (1954, p. 78) has made the useful suggestion that geographical variation in the color and pattern of nighthawks may be an adaptation to geographical differences in the general aspect of soil and vegetation on the

breeding grounds. The color resemblances mentioned between local populations of the two species may be explicable on this theory, at least where they breed in the same habitat.

Certainly in most of the Panamá lowlands where a reddish C. minor breeds the prevailing soil color is reddish—dark reddish clays produced by disintegration of igneous rock. In the heavily eroded and often sandy Llanos de Coclé area, where C. minor may be absent as a breeder and C. acutibennis apparently breeds, the ground color is more conspicuously varied; there are gray and light brown soils as well as dark reddish ones. One may speculate that the existence of marked color variability (even color phases) within some populations of C. acutipennis, in contrast with C. minor, reflects differences in the color variability of their preferred habitats. In regions of sympatry with C. minor, C. acutipennis usually breeds in more barren areas, such as badlands, where the ground may be more exposed by erosion, and where gullies and washes may bring to the surface in close proximity very differently colored strata and soils. Color variability, or even polymorphism, could be adaptive in enabling a semicolonial population to avail itself of breeding sites having very different appearances. Individual variability may be less useful to C. minor, which favors more humid, and generally somewhat more vegetated, environments. In its normal habitat large areas of differently colored bare soil are less likely to be exposed; the soil is usually mixed with humus or leaves or darkened by weathering or shaded by bushes, so that a standardized color, providing contrasts of light and shade, may be more serviceable.

However, adaptation to climatic differences, rather than primarily to soil color, may be the major factor in determining the basic color difference in the various subspecies of nighthawks.

Soil color itself often reflects climate. The palest race of *C. minor* is sennetti of the drier northern Great Plains. The darkest races, the northern nominate minor (particularly the population of the northwest coast) and panamensis, are from the humid areas. The Panamá combination of rufescence and darkness may be a by-product of a physiological adaptation to a warm as well as humid climate. Thus there is a tendency for owls of the genus *Otus* to produce rufous phases in relatively humid regions. Whether color in this nighthawk reflects an adaptation to climate or soil, or both, genetic controls seem to be involved, because even the newly hatched chick of panamensis shows the color tendencies of the race.

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SUMMARY

- 1. A new subspecies of Common Nighthawk, Chordeiles minor panamensis, is described, which breeds in Panamá and probably in Costa Rica.
- 2. The supposedly lost type of *C. virginianus aserriensis* Cherrie is in the American Museum of Natural History. Oberholser's application of this name to the breeding population of south Texas is supported.
- 3. Reasons are advanced for treating the West Indian Nighthawk, C. gundlachii (including vicinus), as a species distinct from C. minor.
- 4. The distribution and variation of *C. minor* and *C. acutipennis* in Middle America are discussed. Both species probably breed in suitable habitats throughout Central America.
- 5. Specimens of *C. acutipennis* taken during the breeding season, or immediately thereafter, in Nicaragua, Costa Rica, and Panamá resemble the South American *C. a. acutipennis* much more than any Mexican population.
- 6. Color parallelism in the two species and possible adaptation to soil color and climate are discussed.

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