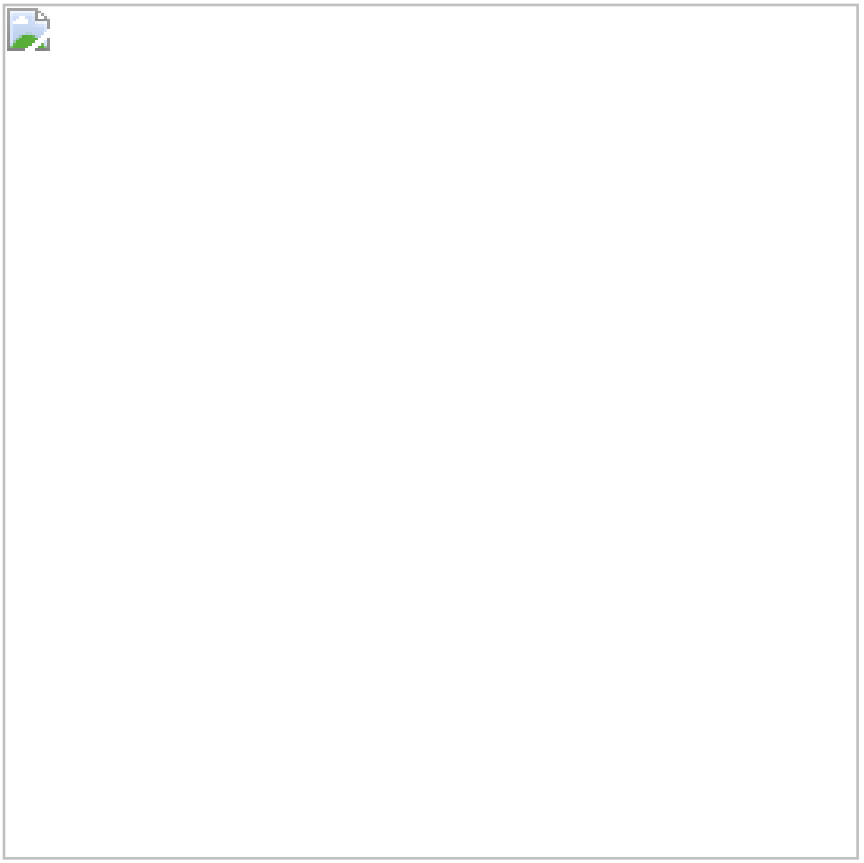

Eye colour is geographically variable in Lesser Roadrunner Geococcyx velox (Wagner, 1836)

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Eye colour is geographically variable in Lesser Roadrunner *Geococcyx velox* (Wagner, 1836)

by John van Dort & Roselvy Juárez

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Summary.—All modern avian world taxonomies currently treat Lesser Roadrunner *Geococcyx velox* as monotypic. Since its description in 1836, however, five subspecies have been described based on tail pattern and underparts colour. These features were later found to be subject to individual and seasonal variation, and in the late 1990s the species was reclassified as monotypic. Here we present a previously overlooked diagnosable character that separates three geographic populations. We evaluated 1,400 photos archived in Macaulay Library and found consistent differences in iris colour, and no evidence of clinal connectivity, suggestive of divergence. We describe sectoral heterochromia for populations of Lesser Roadrunner in Yucatán and Honduras east to Nicaragua, a potential adaptation to foraging in tropical open habitats.

Lesser Roadrunner *Geococcyx velox* is a terrestrial cuckoo with a long graduated tail, buff underparts, and rufous-brown upperparts streaked and spotted white (Moore 1934). It occurs from north-western Mexico south to central Nicaragua, with a disjunct population in the northern Yucatán Peninsula (Peters 1940, Sibley & Monroe 1990). Several roadrunner taxa were first collected and named in the early 19th century; Wagner (1836) was the first to resolve the relationships of these taxa, such as *Cuculus viaticus* M. H. C. Lichtenstein, 1830, *Geococcyx variegata* Wagler, 1831, and *Saurothera marginata* Raub, 1832. Wagner made a comparison separating the smaller species from the larger species already described by Lesson (1829), although he mistakenly thought that Lesser Roadrunner lacks a postocular apterium, an oversight that Hellmayr, who examined Wagner's holotype from 'Mexico', attributed to a skilful covering up of this naked skin with nearby feathering by the taxidermist, who probably thought it was a deficiency in the specimen (Hellmayr 1913). Wagner's description of *Cuculus velox* (1836), based on a specimen from Mexico (Fig. 1) was followed by Hartlaub's description of *Geococcyx affinis* (1844) from Guatemala. Shelley (1891) grouped Wagner's Mexican bird with *Geococcyx mexicanus* (= *G. californianus*) but, as Hellmayr (1913) demonstrated, phenotypically it corresponds to Hartlaub's Guatemalan *affinis*.

Hellmayr recognised the possibility that a larger series of specimens might show Guatemalan populations of Lesser Roadrunner to be separable from Mexican populations, which Moore (1934) subsequently set out to demonstrate. In particular, Moore observed regional variation in tail pattern, noting differences in the size of the white tail spots and the presence or absence and width of a subterminal dark bar on the outer rectrix (Moore 1934). Using these characters, he described two new subspecies—*longisignum* from Honduras and northern Nicaragua, which lacked the subterminal tail bar on the outer rectrix, and *melanchima* of western Mexico, from Sonora to the Isthmus of Tehuantepec, with a broad subterminal tail bar, in addition to nominate *velox*, and the already described *affinis*, both of which possess a subterminal tail bar of intermediate width. This was followed a year later by the description by Carriker & Meyer de Schauensee (1935) of a fifth subspecies with paler

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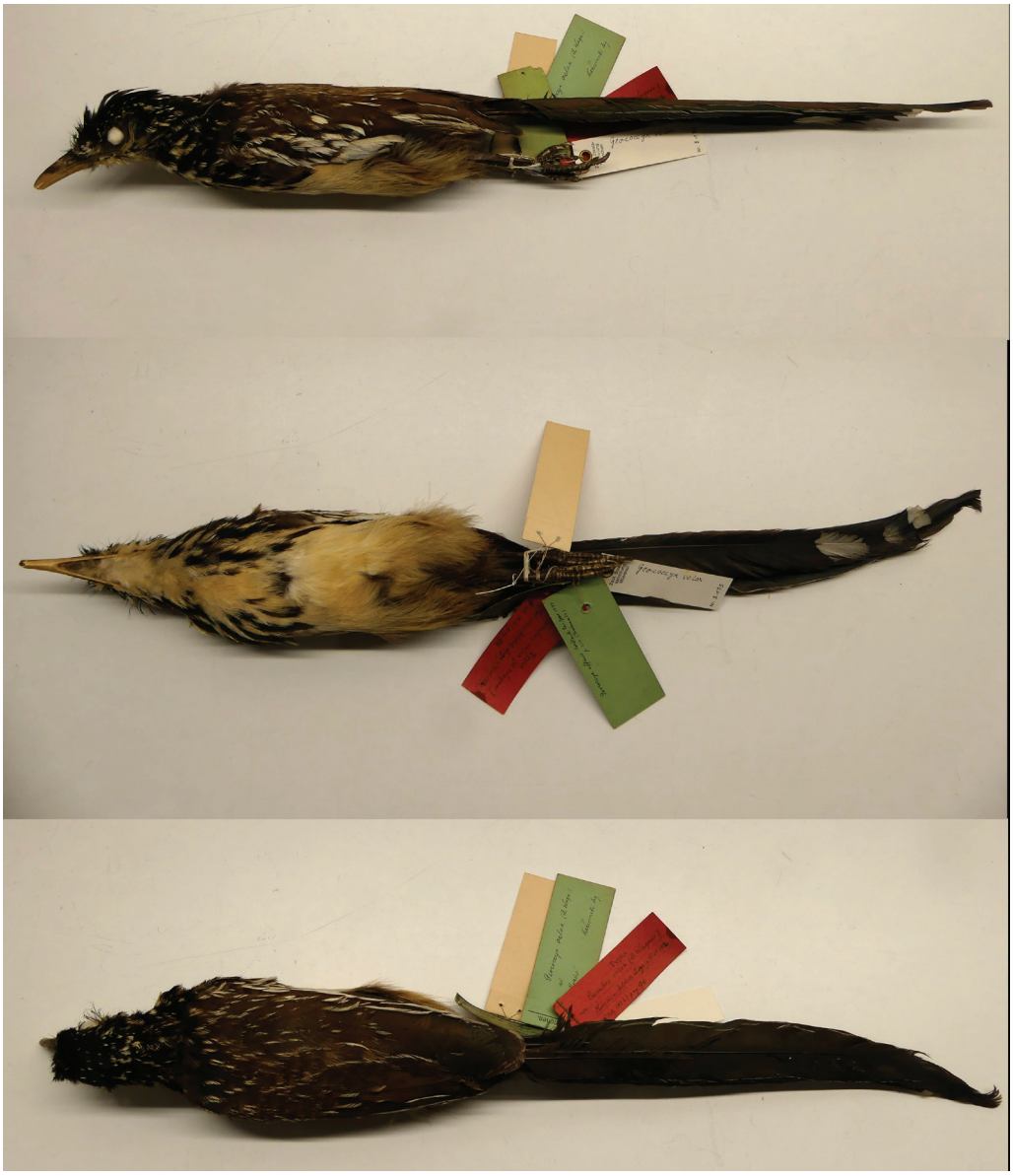

Figure 1. Holotype of Lesser Roadrunner *Geococcyx velox* (Wagner, 1836) collected by Karwinski somewhere near the city of Mexico (precise location unknown), Zoologische Staatssammlung München (ZSM B135); note the strongly discoloured outer rectrix, rendering the black subterminal bar inseparable from the proximal part of the feather (© Guy M. Kirwan)

underparts—*pallidus*—from eastern Guatemala and the Yucatán Peninsula. See Fig. 2 for a map with distributions and type localities for these subspecies. For more than 50 years, this taxonomic arrangement was widely accepted (e.g., Dickey & van Rossem 1938, Peters 1940, Monroe 1968), albeit not universally (e.g. Paynter 1955). Payne (1997, 2005) was first to treat the species as monotypic, arguing that described differences between the subspecies were largely due to individual and seasonal variation, with much overlap between them. This treatment is currently followed by all four global checklists of birds (Dickinson & Remsen 2013, del Hoyo & Collar 2014, Clements *et al*. 2023, Gill *et al*. 2024).

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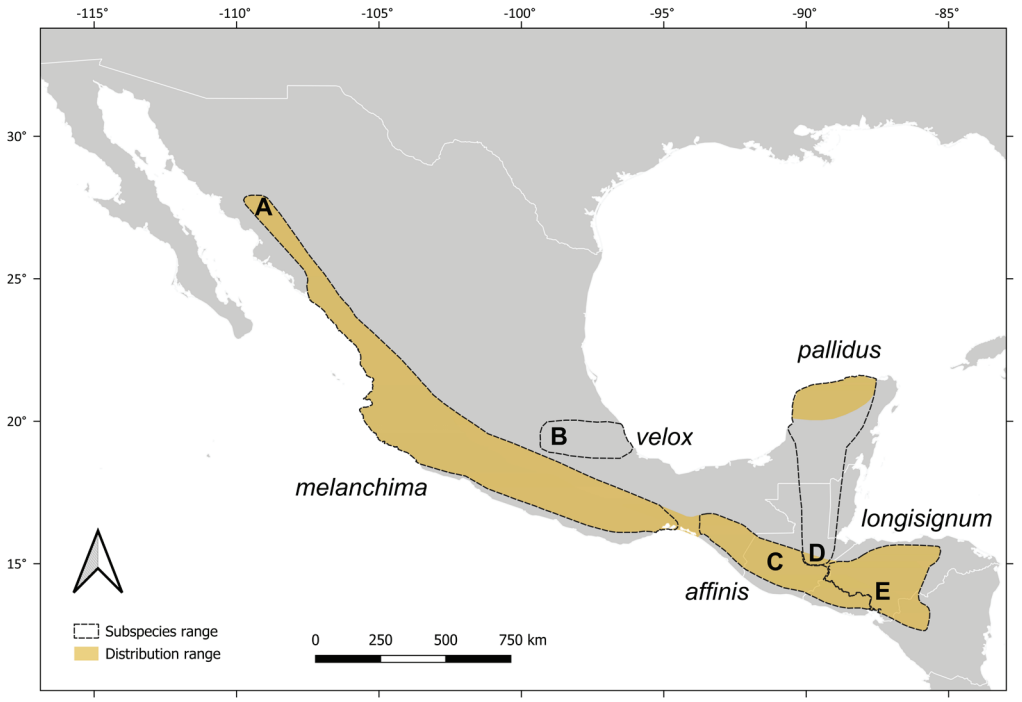

Figure 2. Distribution of Lesser Roadrunner *Geococcyx velox* from BirdLife International & Handbook of the Birds of the World (2022), with ranges of named subspecies currently in synonymy and their type localities per Peters (1940). A: Guirocoba (= Huirocoba), Sonora, Mexico ('*melanchima*'); B: 'outskirts of Mexico City', Distrito Federal, Mexico ('*velox*'); C: 'Guatemala' ('*affinis*'); D = Gualán, Zacapa (Motagua Valley), Guatemala ('*pallidus*'); D: 'Comayabuela' (= Comayaguela), Francisco Morazán, Honduras ('*longisignum*').

Few phylogenetic analyses using molecular characters have hypothesised the evolutionary relationships among cuckoos. The first studies screened a limited set of molecular loci and taxa, and their main contribution was to provide inferences concerning higher-level relationships among the Cuculiformes (Aragón *et al*. 1999, Johnson *et al*. 2000). The most comprehensive study used a larger mtDNA dataset of all extant cuckoos, providing a deeper understanding of relationships at species level (Sorensen & Payne 2005). Although other analyses of the cuckoos have relied partially or entirely on morphological data, apart from a dissertation on the phylogeny of coccyzines, iris colour has not been used explicitly to assess relationships in the Cuculiformes (Hughes 1997, Payne 1997, Sorensen & Payne 2005).

Reviewing our own photographs of Lesser Roadrunner taken in Honduras and comparing them to images archived in the Macaulay Library, Cornell Lab of Ornithology, we noticed that some adults possess a pale ring around the pupil, while others do not. Furthermore, in those individuals with a pale peripupillary ring, its shape differs from that of Greater Roadrunner *Geococcyx californianus*, i.e., it is incomplete. Remarkably, this has largely escaped attention in field guides and other references, which either fail to mention differences in iris colour among Lesser Roadrunner populations, or incorrectly characterise the iris as similar to that of Greater Roadrunner in either written descriptions or colour plates (e.g., Howell & Webb 1995, Payne 1997, Vallely & Dyer 2018). The iris colour in adult Lesser Roadrunner has been described as yellow to brown, with a silvery-whitish ring around the pupil (Ridgway 1916, Dickey & van Rossem 1938, Payne 2005).

Iris colour has rarely been used in taxonomic analyses of birds, mainly due to the difficulty of evaluating or measuring this character after a specimen has been prepared.

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However, with the ongoing rise of digital photography and the quickly expanding capabilities of open-access digital libraries such as Macaulay Library, it is now possible to evaluate iris colour in photographs of live birds on a large scale, and to study this trait from a biogeographical perspective (e.g., Gutiérrez-Expósito 2019, Cardilini *et al*. 2022). Accordingly, we aimed to assess iris colour and pattern and tail pattern in Lesser Roadrunner using digital photographs, and to consider possible implications relative to the previously described taxa, as outlined above.

Methods

To evaluate eye colour and pattern from georeferenced photographs of Lesser Roadrunner, we reviewed all photographs archived in Macaulay Library prior to 1 January 2024. We excluded obvious identification errors, individuals that could not be unambiguously assigned to species in the area of range overlap with Greater Roadrunner, and individuals that were clearly juveniles based on pink gape flanges. We excluded juveniles because we assumed that the pale iris ring, in those populations that show it, is not present immediately post-hatching, analogous to the development of this feature in Greater Roadrunner, which takes up to 85 days (Muller 1971). Development of the pale iris ring in Lesser Roadrunner, however, has not been studied. From each image included in this study, we gathered metadata such as Macaulay Library reference number, country, department/state, date, and coordinates.

To evaluate eye colour and pattern, we classified individuals as pale-eyed (with a narrow pale peripupillary ring); intermediate (ring still visible but darker); dark-eyed (no ring visible); and invisible (Fig. 3). For pale-eyed and intermediate individuals, we noted whether the pale ring was complete, incomplete, or invisible.

In respect of tail pattern, we used as reference an ink drawing made by J. L. Ridgway of the outer rectrices of the described subspecies reproduced as fig. 1 in Moore (1934). To facilitate comparisons, we followed this subdivision and classified all birds in which the tail pattern was visible as 'broad tail bar' for birds with a subterminal tail bar on the outer rectrix visibly broader than Moore's intermediate category B; 'thin tail bar' for all birds matching Moore's intermediate category or had a thinner but still complete subterminal tail bar; and 'no tail bar' for individuals with an incomplete or no subterminal tail bar, corresponding to Moore's category C (Fig. 4). We did not attempt to evaluate other characters used to describe subspecies, such as overall plumage colour, the relative length of the white tip on the outer

Figure 3. Variation in eye colour and pattern in adult of Lesser Roadrunners *Geococcyx velox*; A: dark iris, Oaxaca, Mexico (© Dubi Shapiro; ML 474875311); B: intermediate peripupillary ring, La Paz, Honduras (© Franklin Aguilar; ML 122020681); C: pale peripupillary ring, Choluteca, Honduras (John van Dort; ML 178063861)

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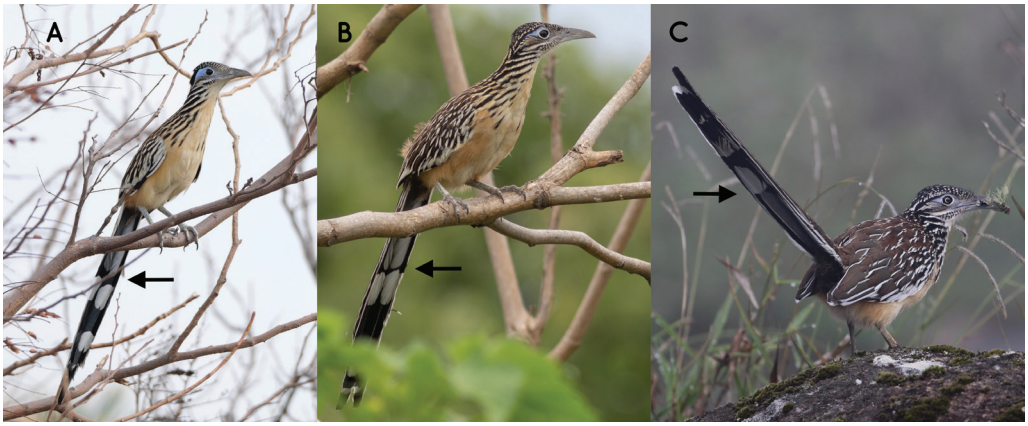

Figure 4. Variation in tail pattern in adult Lesser Roadrunner *Geococcyx velox*; A: broad subterminal bar on outer rectrix, Oaxaca, Mexico (© Micah Riegner; ML 616288095); B: thin subterminal bar on outer rectrix, Guatemala, Guatemala (© Francis Canto Jr.; ML 177836151); C: no subterminal bar on outer rectrix, Choluteca, Honduras (John van Dort; ML 178877761)

rectrix or contrast in the upperparts streaking, as these are more difficult to assess from photos as opposed to museum specimens.

To eliminate pseudo-replication, we then grouped images taken on the same day from the same location into a single observation, and assigned them a unique observation code. If more than one individual was photographed during a discrete observation, we assigned additional observation codes. For some locations, Macaulay Library contains photographs taken on multiple dates. Therefore, to address potential pseudo-replication, we consolidated such observations into a single georeferenced datapoint, even though this may have underestimated the number of individuals photographed at each location, unless clear differences in iris colour or tail pattern were evident between images. We then plotted the data using QGIS over the species' distribution *sensu* BirdLife International & Handbook of the Birds of the World (2022) and other literature (e.g., Howell & Webb 1995, Clements *et al*. 2023).

Results

We evaluated 1,400 images uploaded to Macaulay Library prior to 1 January 2024; of these, we discarded 18 images that were either of Greater Roadrunner or of uncertain identification, as well as 20 images of juveniles, for a total of 1,362 images, representing 659 single observations with a specific date and location. After consolidating the observations based on location in combination with eye colour and tail pattern, we studied at least 470 adults: 459 individuals with a unique location and 11 that showed an eye or tail pattern distinct from an individual already associated with the same locations.

Eye colour and pattern.—We were able to evaluate iris colour in 372 adults, i.e., 79% of the total sample (n = 470): 58% had all-dark eyes (n = 218), 38% had a pale ring in the iris (n = 140) and 4% possessed a ring of intermediate colour in the iris (n = 14). These groups sorted geographically (Fig. 5). We found that practically all adults in western populations, i.e., from Sonora, Mexico to western Honduras, are dark-eyed (Fig 6A). Eastern populations, in the northern Yucatán Peninsula, as well as east of the Honduran Depression to north-western Nicaragua, are pale-eyed (Fig. 6B). There is no overlap between pale-eyed and dark-eyed birds, although we did find occasional intermediate individuals throughout the range, especially where the two populations meet in western Honduras (Fig. 6C). One dark-

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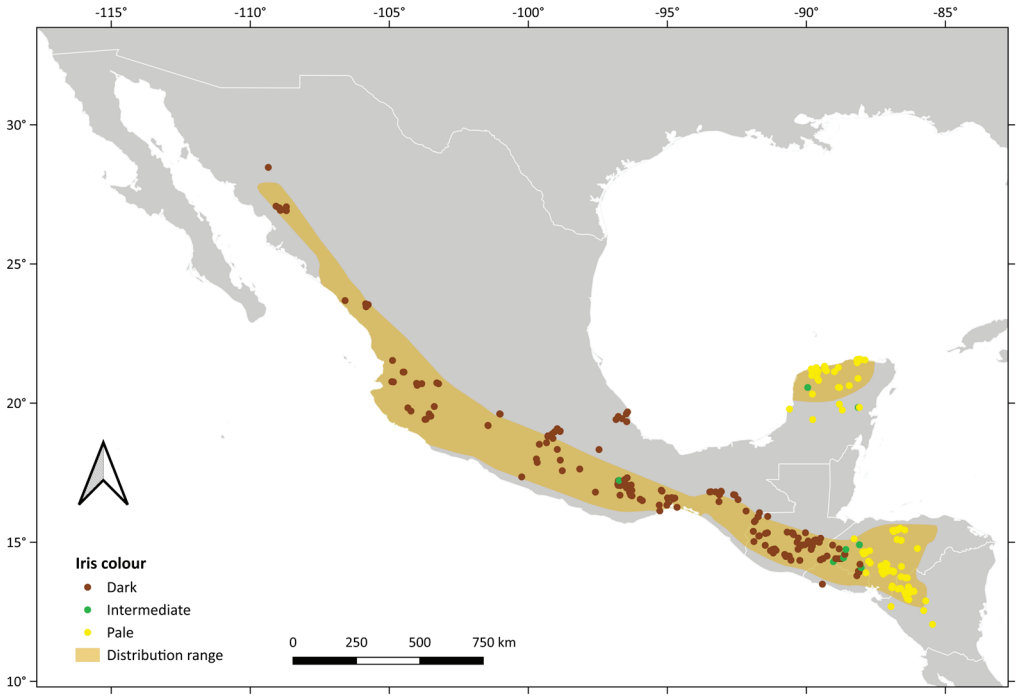

Figure 5: Regional variation in iris colour in Lesser Roadrunner *Geococcyx velox* from multimedia archived in Macaulay Library. Distribution from BirdLife International & Handbook of the Birds of the World (2022).

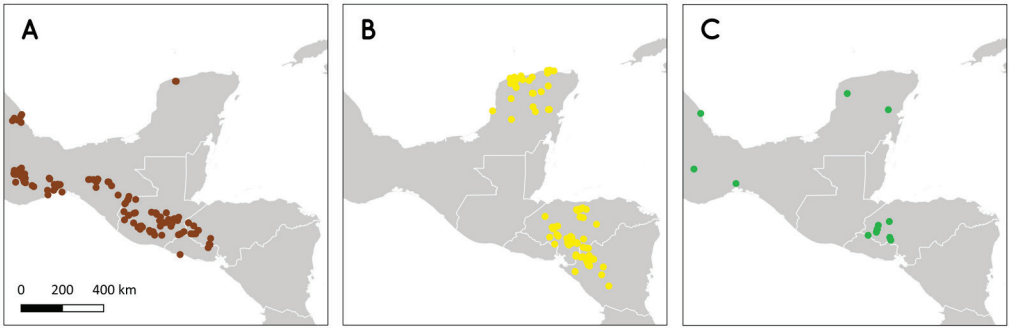

Figure 6. Detailed view of regional variation in Lesser Roadrunner *Geococcyx velox* iris colour showing (A) dark iris; (B) pale iris; and (C) intermediate iris.

eyed individual in the range of pale-eyed birds was photographed at the same location, near Mérida in northern Yucatan, across multiple years, but no pale-eyed individuals were found in the range of dark-eyed populations. For those adults in which the completeness of the peripupillary ring could be evaluated, we found that 99% with pale or intermediate irides had incomplete rings (n = 150). For the two individuals with a complete peripupillary ring, the pattern was similar to Greater Roadrunner, i.e., thinner in the lower frontal part.

Tail pattern.—We were able to evaluate this feature in 114 adults, i.e., 24% of all observations (n = 470): 48% had a broad subterminal bar on the outer rectrix (n = 55) and 31% a thin subterminal bar (n = 35), whilst this bar was absent on 21% (n = 24). Generally, western populations tend to have a broader subterminal bar on the outer rectrix compared to eastern populations, in which this bar is usually thinner or absent, although there was considerable regional overlap (Fig. 7).

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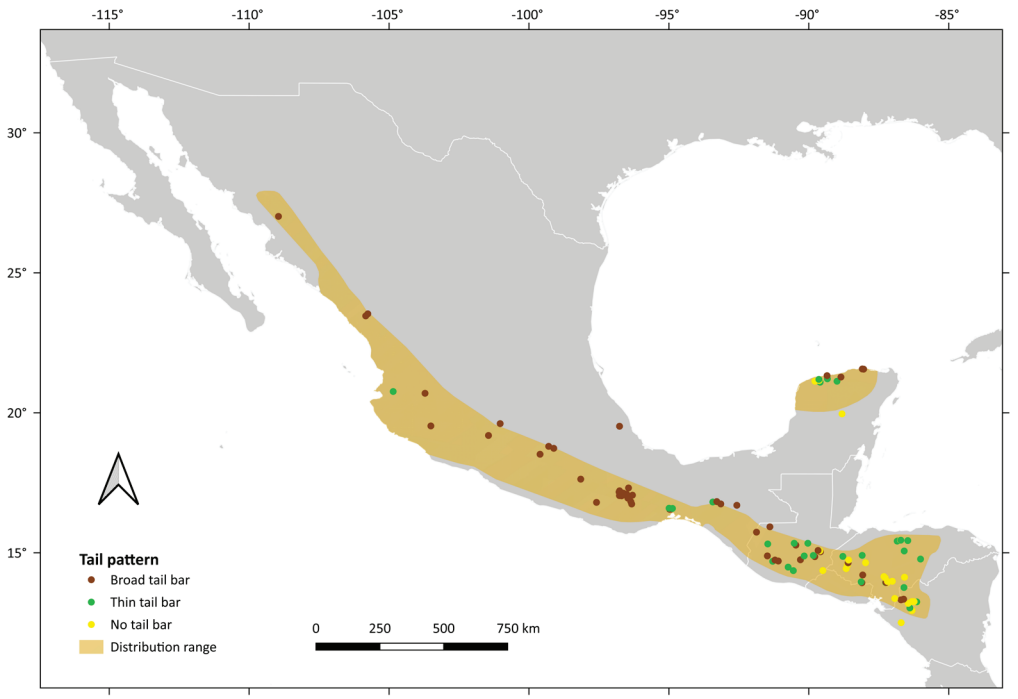

Figure 7. Regional variation in the pattern of the subterminal bar on the outer rectrix in Lesser Roadrunner *Geococcyx velox* from multimedia archived in the Macaulay Library. Distribution from BirdLife International & Handbook of the Birds of the World (2022).

Discussion

Earlier classifications of Lesser Roadrunner taxa were based primarily on tail pattern and underparts coloration (Moore 1934, Carriker & Meyer de Schauensee 1935). The last-named authors were early critics of Moore's emphasis on tail pattern, which they considered to be subject to individual variation, a finding corroborated since by many others (e.g., Blake 1950, Paynter 1955, Payne 2005, Howell 2010). Similarly, differences in underparts coloration were later interpreted as the result of seasonal variation, i.e., darker fresh plumage vs. paler worn plumage, and it was proposed to treat Lesser Roadrunner as monotypic (Payne 1997, 2005, Erritzøe *et al*. 2012).

Our results confirm Moore's finding that western populations tend to show a broader subterminal band on the outer rectrix, compared to eastern populations in which this band is thinner or absent. Nevertheless, we also found support for the contention of Blake and others that this character varies individually and that atypical birds occur throughout the range. We found variation in underparts colour to represent seasonal wear, as can be appreciated in photographs taken at the same location in different months (e.g., ML 120216781 showing a mix of fresh and worn plumage in October, and ML 612638988 in fresh plumage in December). However, pronounced regional differences in the iris colour of Lesser Roadrunner, especially the peripupillary ring, have not been described or considered taxonomically significant previously.

Our analysis demonstrates the existence of three groups: a dark-eyed group in north-western Mexico to western Honduras, and two pale-eyed groups: one in western Honduras to central Nicaragua, and one in the northern Yucatán Peninsula. The latter is

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wholly allopatric, but the first two groups appear to be parapatric in western Honduras, with a narrow zone in the Honduran Depression where a few intermediates occur (Figs. 5–6). These distributions are suggestive of introgression and/or incomplete lineage sorting between two species, and merit further investigation (Helbig *et al.* 2002, Donegan 2018). A single dark-eyed individual in the range of the pale-eyed group in the Yucatán (Fig. 6A) suggests that, in this population, dark irides may be recessive to pale iris colour, as in domestic chickens (Smyth 1990, Corbett *et al*. 2024). Paynter (1955) correctly questioned whether *pallidus* is valid, since specimens from its purported range are extremely variable and inseparable from *affinis* in eastern Chiapas. He also considered noteworthy that the wide rainforest gap between populations in the northern Yucatán and in the Motagua Valley in Guatemala had not resulted in any visible plumage variation (Paynter 1955). Our findings, however, suggest that these populations do differ dramatically: Guatemalan populations are dark-eyed and Yucatán populations are pale-eyed.

The most comprehensive molecular phylogeny of the Cuculiformes using mtDNA sampled only a single Lesser Roadrunner specimen, from Nicaragua, i.e., from one of the pale-eyed groups, and work at finer scales remains to be done (Sorensen & Payne 2005). Compared with Greater Roadrunner, which typically has a complete pale ring around the pupil, the pale ring in those populations of Lesser Roadrunner that show it, is nearly always incomplete, with a dark area in the lower frontal part of the iris (sectoral heterochromia). The adaptive significance of this trait is untested, but we hypothesise that the position of the darker area, similar to that observed in other open-area foragers such as buttonquail (*Turnix*) and lapwings (*Vanellus*), facilitates foraging in open environments at tropical latitudes, where sun glare reflection may impede prey detection (Gutiérrez-Expósito 2019, Cardilini *et al*. 2022). Sectoral heterochromia, typical of eastern populations of Lesser Roadrunner, had not been described for this species or illustrated in field guides. The two recent cuckoo monographs describe iris colour in Lesser Roadrunner as yellow to brown with a silvery-white ring around the pupil, but do not describe this ring as incomplete, nor do they ascribe regional or taxonomic significance to this character (Payne 2005, Erritzøe *et al*. 2012). A lack of awareness of the regional significance of eye colour and pattern possibly led Erritzøe *et al*. (2012) to mislabel both photographs of Lesser Roadrunner with each other's locations; one of these photographs even shows a Greater Roadrunner. Most modern works incorrectly illustrate Lesser Roadrunner with the same iris colour and pattern as Greater Roadrunner, i.e., with a complete pale peripupillary ring (Howell & Webb 1995, Payne 1997, Vallely & Dyer 2018, Soberanes-González *et al*. 2020). Whilst the pale peripupillary ring in the iris of Greater Roadrunner has been described (Payne 2005, Erritzøe *et al*. 2012, Hughes 2020), we were unable to find mention of its uneven width, being generally thinner in the lower frontal area (radial asymmetry). A review of high-resolution photographs archived in Macaulay Library suggests that practically all Greater Roadrunners show a pale inner ring of uneven width, perhaps an adaptation to foraging on the ground in arid open environments.

Iris colour, especially when bright, plays an important role in social signalling to indicate age, sex and mate quality (Craig & Hulley 2004, Corbett *et al*. 2024). For Lesser Roadrunner populations that develop incomplete pale rings, this may be an example of intraspecific signalling, indicating age and sexual maturity in a taxon that otherwise does not differ between age classes (Corbett *et al*. 2024). On the other hand, for those populations whose irides are dark, iris colour may possess an interspecific signalling function, i.e., an isolating mechanism between dark-eyed Lesser and pale-eyed Greater Roadrunners, as in other closely related avian taxa with sympatric distributions, such as storks and gulls (Pierotti 1987, Rodríguez-Rodríguez & Negro 2021). eBird data show that in Mexico, the two

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taxa are largely parapatric, but with extensive sympatry in Sonora, Sinaloa, Nayarit, Jalisco, Michoacán, Morelos and Puebla, *contra* Soberanes-González *et al*. (2020).

Our study highlights a previously undescribed diagnosable character in Lesser Roadrunner populations, calling into question current taxonomy and inviting further study along phenotypic and molecular lines. In many avian families, iris colour is a highly conserved trait, and for several cryptic species it has proven a useful predictor of taxonomic divisions at species rank, e.g., in boubous (Voelker *et al*. 2010), bulbuls (Shakya *et al*. 2019) and scrubwrens (Cake 2019). Similarly, in Cuculidae, recent mtDNA work separated members of the genus *Coccycua*—which have red eyes—from dark-eyed *Coccyzus* (Hughes 2006). We found no apparent clinal connectivity in iris colour for two parapatric populations of Lesser Roadrunner, suggesting that at least some of the groups we identified may be species.

Acknowledgments

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