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RESEARCH ARTICLE

The changing diversity and distribution of dry forest passerine birds in northwestern Peru since the last ice age

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ABSTRACT

The role of Quaternary glacial–interglacial intervals in shaping the diversity and distribution of Neotropical species has been the focus of considerable research. The Neotropics sustain the highest passerine diversity on Earth, but little is known about this region's historical biogeography based on fossils. To assess how passerine species were affected by Quaternary climate fluctuations, we identified 625 late Pleistocene fossils (individual fossilized bones) from the now arid and faunally depauperate Talara Tar Seeps in northwestern Peru. Of the 21 passerine species identified, only 2 likely live at the site now; the remaining 19 species require more mesic conditions. Species identified included members of the Thamnophilidae (antbirds), Melanopareiidae (crescentchests), Tyrannidae (flycatchers), Hirundinidae (swallows), Mimidae (mockingbirds), Thraupidae (seedeaters, "finches"), Emberizidae (sparrows), and Icteridae (blackbirds). Nearly half of the individual fossils and 8 of the 21 species were icterids, including 3 extinct species (1 previously described, 2 new). The late Pleistocene passerine community at Talara, which was nonanalog to any modern community, suggests that the site once supported savanna, grasslands, and forests during the last glacial interval, which are absent near Talara today. Quaternary climate change and the collapse of the community of large mammals had a major influence on the community composition and the geographic ranges of passerine species in northwestern Peru.

Keywords: climate change, extinction, Neotropical diversity, passerine fossils, Pleistocene, range dynamics, Tumbes

Diversidad y distribución cambiante de aves paseriformes de bosques secos en el noroeste de Perú desde la última edad de hielo

RESUMEN

Un foco de investigación importante ha sido el rol de los intervalos glaciares-interglaciares del Cuaternario como agentes modeladores de la diversidad y la distribución de las especies neotropicales. El Neotrópico sustenta la más alta diversidad de paseriformes en la Tierra, pero poco se sabe sobre su biogeografía histórica basada en fósiles. Para evaluar cómo las especies de paseriformes fueron afectadas por las fluctuaciones climáticas del Cuaternario, identificamos 625 fósiles del Pleistoceno tardío (huesos individuales fosilizados) provenientes de Talara Tar Seeps, un área del noroeste de Perú actualmente árida y depauperada de fauna. De las 21 especies paseriformes identificadas, solo dos probablemente viven en la actualidad en el sitio; las restantes 19 especies necesitan condiciones más mésicas. Las especies identificadas incluyen miembros de los Thamnophilidae, Melanopareiidae, Tyrannidae, Hirundinidae, Mimidae, Thraupidae, Emberizidae e Icteridae. Cerca de la mitad de los fósiles individuales y 8 de las 21 especies son ictéridos, incluyendo tres especies extintas (una descrita previamente, dos nuevas). La comunidad de paseriformes del Pleistoceno tardío de Talara, que no tiene un análogo con ninguna comunidad moderna, sugiere que el sitio en el pasado albergó sabanas, pastizales y bosques durante el último intervalo glaciar, los cuales están ausentes cerca de Talara en el presente. El cambio climático del Cuaternario y el colapso de la gran comunidad de mamíferos tuvo una gran influencia en la composición de la comunidad y en los rangos geográficos de las especies de paseriformes del noroeste de Perú.

Palabras clave: Cambio climático, dinámica de rangos, diversidad neotropical, extinción, fósiles paseriformes, Pleistoceno, Tumbes

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INTRODUCTION

The extraordinary biotic diversity found in the Neotropics is the result of numerous mechanisms that have acted over millions of years. The uplift of the Andes throughout the Cenozoic (past 65 million years) divided the ranges of taxa, changed soils and the direction of rivers, and led to the formation of numerous biomes (Graham 2009, Hoorn et al. 2010). These changes affected the entire South American continent, even lowland Amazonia, where plants and animals would have experienced novel atmospheric circulation and new riverine barriers (Rull 2011, Ribas et al. 2012). Over more recent time scales, the ~22 glacial–interglacial cycles during the Quaternary (2.6–0.0 mya) also have shaped modern diversity and distributions in the region (Colinvaux et al. 1997, 2000, Hoorn et al. 2010, Cohen and Gibbard 2011, Rull 2011).

Haffer (1969) hypothesized that Neotropical rainforest birds underwent allopatric speciation in habitat refugia (isolated areas of humid forest) during Pleistocene glacial periods, when dry vegetation was believed to have dominated and subdivided the lowland Amazonian rainforest. Allopatric populations of birds diverged and remained reproductively isolated, even after secondary contact when rainforest re-expanded during interglacial periods. However appealing, this hypothesis has received little support from phylogenetic studies across numerous taxa, which suggest that many (but not all) Amazonian plants and vertebrates diversified across both the Neogene (25.0–2.6 mya) and the Quaternary (Hoorn et al. 2010, Rull 2011).

Numerous lowland rainforest plant genera have been present in Amazonia since at least the late Miocene (Colinvaux and Oliveira 2001). Furthermore, pollen samples from sediment cores do not reveal lowland dry-habitat indicator plants in Amazonia during glacial periods, even though some cool-adapted Andean plants did occur in the western Amazon basin (Colinvaux et al. 1996a, 1996b, 1997, 2000). Nevertheless, pollen data show evidence of more expansive open habitats near the southern fringe of the Amazon Basin in glacial times (van der Hammen 1972, Absy et al. 1991). This presents the possibility that Quaternary climate fluctuations had a stronger influence on diversity and distributions in biogeographical regions outside Amazon Basin rainforests.

Relative to rainforests, Neotropical dry forests sustain lower diversity, yet greater levels of endemism (Janzen 1988, Stotz et al. 1996, Pennington et al. 2006). Despite hypotheses regarding the expansion and contraction of these dry forests and savannas during glacial–interglacial cycles (Prado and Gibbs 1993, Pennington et al. 2000), the role of Quaternary climate change on their biotic diversity and distributions is little studied, except for plants (but see Smith et al. 2012, Werneck et al. 2012). Determining the distributions of characteristic Neotropical dry forest and savanna organisms during glacial intervals would provide insight into the historical vs. modern connectivity of these habitats. Late Pleistocene fossils of Neotropical birds, for example, are tangible evidence of historical diversity, past species distributions, and environmental conditions (Steadman and Mead 2010, Steadman et al. 2015). Small vertebrate fossils, avian or otherwise, can be excellent indicators of past fine-scale habitat distributions, and furthermore often reveal nonanalog paleocommunities, i.e. sets of species that no longer exist sympatrically today, even when extinct species are excluded (Steadman et al. 1994, Stafford et al. 1999, Semken et al. 2010).

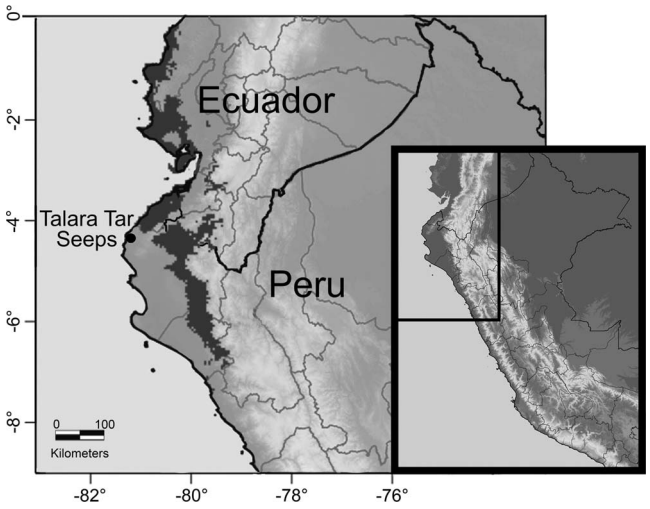


FIGURE 1. Location of the Talara Tar Seeps (4°39′S, 81°08′W) in northwestern Peru. The approximate distribution of Tumbesian tropical dry forest is shaded in dark gray. The Andes are shaded in light gray to white.

Songbirds (passerines; Passeriformes) constitute more than 50% of the world's living bird species and are hyperdiverse in the Neotropics (Stotz et al. 1996, Brumfield 2012), yet have a very limited fossil record. Here, we report 600+ passerine fossils from the Talara Tar Seeps in northwestern Peru. Today, the site is arid (desert) with the nearest dry forest ~50 km away. The passerine fossils from Talara present a unique opportunity to reconstruct not only the late Pleistocene songbird community but also the associated climatic conditions and habitats at the site, thereby elucidating the role of Quaternary glacial–interglacial cycles in shaping a distinctive Neotropical bird community.

METHODS

The Talara Tar Seeps (4°39′S, 81°08′W) are located at ~140 m elevation and ~20 km southeast of the coastal city of Talara (Figure 1). Today, the area around the site (<30

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cm mean annual rainfall) sustains a depauperate flora and fauna. Dry forests, with considerable biotic diversity and a remarkable number of endemic taxa, are found northeast, east, and southeast of Talara at higher elevations ~50 km inland with higher precipitation (Parker et al. 1995, Stotz et al. 1996). Talara lies within the Tumbesian Region, which is an area of high endemism in northwestern Peru and southwestern Ecuador, characterized by gradients from coastal deserts to more inland dry and semideciduous forests.

Based on conventional radiocarbon (^{14}C) dating of associated pieces of wood, the fossils at Talara are late Pleistocene in age (last glacial interval; between 13,616 ± 600 and 14,418 ± 500 ^{14}C years before present [BP]; Churcher 1966). Using a standard calibration database (Heaton et al. 2009, Reimer et al. 2009), these two ^{14}C determinations translate to 15,903 ± 808 and 17,054 ± 816 calendar years (cal) BP (~15,000 to 18,000 cal BP, or at the close of the last glacial maximum). Because stratigraphic mixing can occur in tar seeps as trapped animals sink while struggling in tar of varying viscosity (Shaw and Quinn 1986, Friscia et al. 2008), we attempted to augment the chronology of Talara by ^{14}C-dating individual bird fossils from Talara. We were not successful because inadequate collagen remained in the bones. The age of the bird fossils from Talara is confidently late Pleistocene, centered on ~15,000–18,000 cal BP.

The Talara Tar Seeps fossils that we studied were excavated by A. G. Edmund and field crew in 1958 (Churcher 1959); they are housed at the Royal Ontario Museum (ROM), Toronto, Canada. While the nonpasserine fossils from Talara were studied by Campbell (1979), the passerine fossils were sorted by size categories and element but not examined further until our study. By "fossil," we are referring to individual fossilized bones, e.g., humerus, coracoid, rostrum. We compared the fossils directly with modern skeleton specimens from the Florida Museum of Natural History, University of Florida (UF), Louisiana State University Museum of Natural Science (LSUMNS), and the National Museum of Natural History (USNM), and with fossils of extinct icterids housed in the UF Vertebrate Paleontology Division. If available, a series of skeletons of both males and females was used for identifications. Specimens listed in the Appendix represent average osteological characteristics for the specimens examined. The fossils also were evaluated using original descriptions of extinct species (Miller 1929, 1932, 1947). The osteological characters that we used for identification are given in the Appendix. All ROM catalog numbers are listed in Supplemental Material Table S12. Osteological nomenclature follows Baumel et al. (1993), supplemented by Howard (1929).

Information on habitats and geographic ranges of extant species is based on Schulenberg et al. (2007), Ridgely and Tudor (2009), and our own field observations. We visited the site twice in November 2011 and observed a very depauperate bird community (see Results). Because of the large number (~2,800) of passerine fossils recovered at Talara, we focused primarily on the most diagnostic skeletal elements of the skull, bill, shoulder girdle, and wing.

RESULTS

Based on scored osteological characters, we identified 625 fossils from the Talara Tar Seeps, representing up to 25 taxa (family level and below) and at least 21 species (Table 1; see Appendix Tables 2–11 for character matrices). We regard 3 of the species (all icterids; see below) as extinct. Only 2 of the 18 extant passerine species (Long-tailed Mockingbird [*Mimus longicaudatus*] and Cinereous Finch [*Piezorina cinerea*]) occur at the site today. Three other extant species recorded as fossils (Sulphur-throated Finch [*Sicalis taczanowskii*], Parrot-billed Seedeater [*Sporophila peruviana*], and Tumbes Sparrow [*Rhynchospiza stolzmanni*]) may also occur there sporadically, such as during El Niño events. The only other species that we recorded at Talara during our 2 visits was the Necklaced Spinetail (*Synallaxis stictothorax*), which we did not find as a fossil.

The remaining 13 extant species certainly are extralocal. The Yellow-billed Cacique (*Amblycercus holosericeus*; Figure 2) shows the greatest range shift. In northwestern Peru, *A. holosericeus* lives in semideciduous forests inland and at higher elevations than Talara. Its habitat preferences in northwestern Peru differ from populations elsewhere, which tend to occur in the understory of secondary forest, bamboo thickets, and fields (Fraga 2011b). The Elegant Crescentchest (*Melanopareia elegans*), Collared Antshrike (*Thamnophilus bernardi*), Social Flycatcher (*Myiozetetes similis*), Baird's Flycatcher (*Myiodynastes bairdii*), and Yellow-tailed Oriole (*Icterus mesomelas*) also are indicators of dry, semideciduous, and gallery forests (Table 1, Appendix Figures 3 and 4). The Peruvian Meadowlark (*Sturnella bellicosa*), Scrub Blackbird (*Dives warszewiczi*), martin (*Progne* sp.), Tumbes Swallow (*Tachycineta stolzmanni*), Chestnut-collared Swallow (*Petrochelidon rufocollaris*), and Barn Swallow (*Hirundo rustica*) occupy grasslands, farms, savannas, and forest edges.

Eight species of icterid were recovered from Talara, 3 of which are extinct. Six of the 10 most numerous passerine species identified are icterids (Peruvian Meadowlark, n = 183; Shiny Cowbird [*Molothrus bonariensis*], n = 87; Scrub Blackbird, n = 41; the extinct *Euphagus magnirostris*, n = 36; the extinct troupial *Icterus icterus* s.l., n = 23; and the extinct Talara cowbird [*Molothrus* nov. sp.], n = 15). One of the extinct icterids (*E. magnirostris*) from Talara was first described from the Rancho La Brea Tar Seeps in Los Angeles, California, USA, based on a mandible larger and

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TABLE 1. Passerine fossils identified from the Talara Tar Seeps, northwestern Peru. Modern habitat preferences are from Schulenberg et al. (2007), Ridgely and Tudor (2009), and our observations. "Tumbesian" refers to the region of arid and semi-arid habitats in northwestern Peru and southwestern Ecuador, west of the Andes. Taxa in brackets [] are not necessarily different from those identified with more taxon-specific resolution. If bracketed species are different from identified taxa, then the fossils represent 24 total species; if they are not different, then 21 species are represented. To be conservative, we assume that the bracketed species are not different species in the totals row under the "Occurs at site today" column. Extinct species are indicated by a dagger (†). N/A = not applicable (indeterminate).

Family	Taxon	Total fossils	Occurs at or near site today	Modern habitat preferences	Modern range
Thamnophilidae	*Thamnophilus bernardi*	4	No	Arid scrub, dry forest	Tumbesian + Marañon Valley endemic
Melanopareiidae	*Melanopareia elegans*	1	No	Arid scrub, dry forest	Tumbesian endemic
Tyrannidae	*Myiozetetes similis* cf. *grandis*	1	No	Second growth, forest edge	Widespread; subspecies endemic to Tumbes
Tyrannidae	*Myiodynastes bairdii*	2	No	Arid scrub, dry forest	Tumbesian endemic
Hirundinidae	*Progne* sp.	5	No	Open to semiopen areas	N/A
Hirundinidae	*Tachycineta stolzmanni*	3	No	Open to semiopen areas	Tumbesian endemic
Hirundinidae	*Petrochelidon rufocollaris*	47	No	Towns, farms, open to semiopen habitats	Tumbesian endemic
Hirundinidae	*Hirundo rustica*	3	No	Open to semiopen areas	Widespread migrant
Hirundinidae	[Hirundinidae sp.]	2	N/A	N/A	N/A
Mimidae	*Mimus longicaudatus*	22	Yes	Arid scrub, light woodlands, gardens	Widespread
Thraupidae	*Piezorina cinerea*	1	Yes	Desert scrub	Tumbesian endemic
Thraupidae	[*Sicalis* sp.]	112	N/A	N/A	N/A
Thraupidae	*Sicalis taczanowskii*	22	Possible	Desert scrub	Tumbesian endemic
Thraupidae	*Sporophila peruviana*	1	Possible	Arid scrub, agricultural areas, grassy habitats	Widespread
Thraupidae	[*Sporophila* sp.]	1	N/A	N/A	N/A
Emberizidae	*Rhynchospiza stolzmanni*	2	Possible	Dry scrub, dry forest	Tumbesian endemic
Icteridae	*Amblycercus holosericeus*	5	No	Semideciduous forest	Widespread
Icteridae	[*Icterus* sp. (oriole)]	3	No	N/A	N/A
Icteridae	*Icterus icterus* s.l. †	23	No	Extinct species or subspecies	Unknown
Icteridae	*Icterus mesomelas*	3	No	Dry forest, scrub	Widespread
Icteridae	*Dives warszewiczi*	41	No	Arid scrub, fields, gardens, towns	Western Peru + Marañon Valley endemic
Icteridae	*Euphagus magnirostris* †	36	No	Extinct	Extinct
Icteridae	*Molothrus bonariensis*	87	No	Agricultural fields, forest edges	Widespread
Icteridae	*Molothrus* sp. nov. †	15	No	Extinct	Extinct
Icteridae	*Sturnella bellicosa*	183	No	Cultivated areas, scrub, grassy areas	Widespread
Total fossils		625	2 Yes, 3 Possible,		
Total species		21–24	16 No		

more robust than in either extant species of *Euphagus* (Miller 1929, Steadman et al. 2015). From Talara, we identified *E. magnirostris* mandibles and postcranial material sharing qualitative osteological characters with extant *E. carolinus* (Rusty Blackbird) and *E. cyanocephalus* (Brewer's Blackbird; Figure 5, Appendix Table 5). The extinct cowbird (*Molothrus* nov. sp.) is known thus far only from the fossils that we identified from Talara (Figures 6, 7). It is intermediate in size between the large Giant Cowbird (*M. oryzivorus*), a widespread species that occurs only in humid forests in the Tumbesian region, and the much smaller Shiny Cowbird, another widespread species known from the Tumbesian region, both living and fossil. The troupial fossils at Talara represent a new species or subspecies of *Icterus icterus* s.l. (Figure 8). The species and subspecies of troupial vary considerably in body size (Jaramillo and Burke 1999, Remsen et al. 2014) and osteological characters. The Talara troupial is larger than the Orange-backed Troupial (*I. croconotus*) found east of the Andes in Peru and Bolivia (*I. c. croconotus* and *I. c. strictifrons*) and is more similar in size to the Venezuelan Troupial (*I. icterus*) of Venezuela and Colombia. The 3 extant troupial species prefer dry habitats and gallery forests in the Amazonian lowlands in Peru and Bolivia,

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FIGURE 2. The humerus (above) and coracoid (below) of fossil (left) and modern (right) specimens of blackbirds (Icteridae). (**A**) *Dives warszewiczi* fossil humerus ROM 70065, coracoid ROM 70085, modern LSUMZ 157416. (**B**) *Sturnella bellicosa* fossil humerus ROM 70238, coracoid ROM 70307, modern UF 47467. (**C**) *Amblycercus holosericeus* fossil humerus ROM 69934, coracoid ROM 69930, modern UF 33277 (old PB catalogue number 29362). PB = collection of Pierce Brodkorb; now in UF (Florida Museum of Natural History, University of Florida) collection. ROM = Royal Ontario Museum; LSUMZ = Louisiana State University Museum of Natural Science. Scale bars = 10 mm.

northern Venezuela, northeastern Colombia, and eastern Brazil (Ridgely and Tudor 2009).

The remaining passerine fossils at Talara represent various species of Thamnophilidae, Melanopareiidae, Tyrannidae, Hirundinidae, Mimidae, Thraupidae, and Emberizidae (Table 1). Numerous cranial elements represent either a new species of *Sicalis* (Thraupidae) or a slightly larger-billed variety of Sulphur-throated Finch (*S. taczanowskii*; Appendix Figure 9). Interspecific plasticity in shape and size of the bill is famously exemplified within related genera of thraupid finches and cardinalids such as *Geospiza*, *Sporophila*, and *Passerina* (Steadman 1982, Steadman and McKitrick 1982, Grant 1985). Pending successful extraction of DNA from tar seep fossils (Gold et al. 2014), it will be difficult to evaluate the species-level systematics of these *Sicalis* fossils, especially given that *Sicalis* species have extraordinarily similar postcranial osteological features (Appendix Table 6, Appendix Figure 9). Most of the postcranial fossils that have *Sicalis* characteristics are larger than modern *S. taczanowskii*, but overlap in size with *S. flaveola* (Saffron Finch). Therefore, we were able to identify these elements only to genus. A few postcranial fossils ($n = 22$) are probably *S. taczanowskii*. The Parrot-billed Seedeater (*Sporophila pervuiana*) also was found at Talara (a single fragmentary fossil rostrum; Appendix Figure 9). This species forages primarily on grass seeds (Jaramillo 2011) and is further evidence of the presence of grassy habitats at the site in the late Pleistocene.

Three species of martin (*Progne*; Hirundinidae) occur in northwestern Peru today. Each can be found near lakes, rivers, agricultural fields, and towns (Ridgely and Tudor 2009). We could not identify the *Progne* fossils to the species level because of a lack of comparative material

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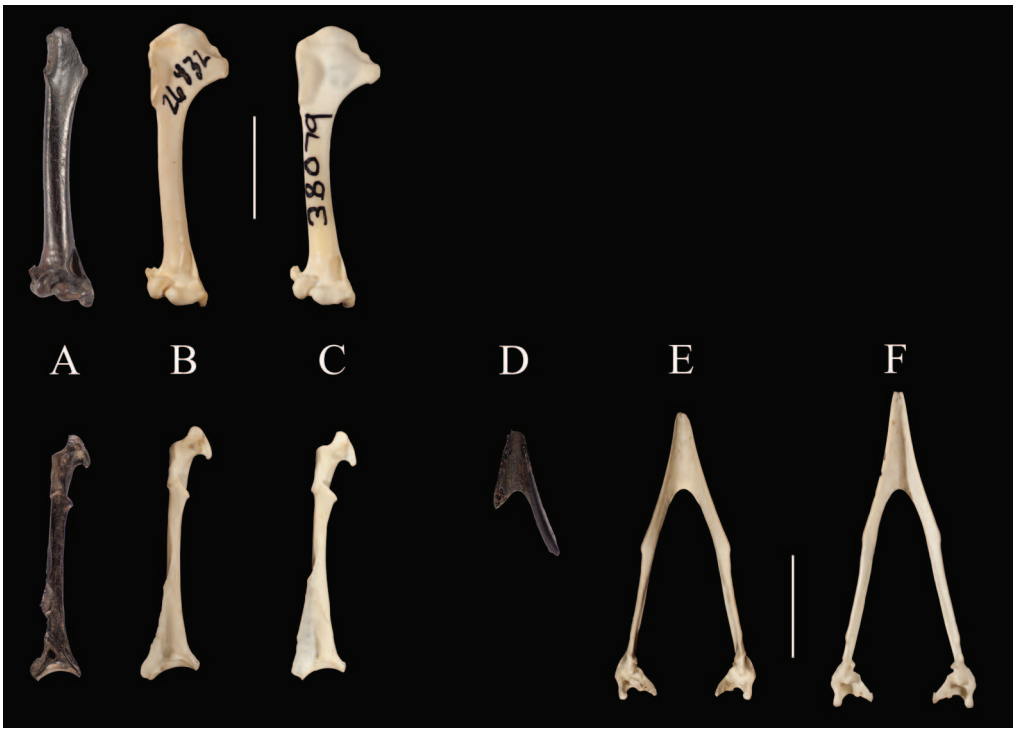


FIGURE 5. The humerus (**A**–**C**, upper), coracoid (**A**–**C**, lower), and mandible (**D**–**F**) of 3 species of *Euphagus*. (**A**, **D**) The extinct *Euphagus magnirostris* ROM catalog numbers 70107 (humerus), 70129 (coracoid), 70104 (mandible). (**B**, **E**) *Euphagus carolinus* UF 31110 (old PB catalogue number 26432). (**C**, **F**) *Euphagus cyanocephalus* UF 31114 (old PB catalogue number 38079). Scale bars = 10 mm.

from the region. Two species of swallow are represented as fossils at Talara, the Tumbes Swallow (*Tachycineta stolzmanni*) and the Chestnut-collared Swallow (*Petrochelidon rufocollaris*; Appendix Table 8, Appendix Figure 10). As with the martins, the modern habitat preferences of these 2 swallows are fairly ubiquitous and generalized. The Barn Swallow (*Hirundo rustica*) is a migratory species that breeds in North America and winters across Central and South America (Appendix Figure 10).

DISCUSSION

Late Pleistocene Climate and Habitats

The transition from the last glacial interval of the late Pleistocene to the modern interglacial interval (Holocene) dramatically changed the landscape of northwest Peru. Our findings from passerine bird fossils supplement the substantial information from sediments, archaeological remains, nonpasserine fossils, and megamammal fossils that argues for more diversity and more mesic climatic conditions in the region in the past (Lemon and Churcher 1961, Campbell 1976, 1979, 1982, Richardson 1978, Sandweiss 2003). Sedimentary evidence from 10 km east of the fossil site suggests the presence of permanent to semipermanent streams in this currently waterless region during the late Pleistocene (Lemon and Churcher 1961, Campbell 1979). A large number of the 6,200 nonpasserine bird fossils identified from the Talara Tar Seeps are from freshwater species, including grebes, herons, cormorants, ducks, geese, sandpipers, and plovers, not to mention other identified aquatic taxa such as amphibians, turtles, crocodilians, and mollusks (Campbell 1979). While other nonpasserine species found as fossils are characteristic of grassland or savanna (Black-chested Buzzard-Eagle [*Geranoaetus melanoleucus*], Short-eared Owl [*Asio flammeus*]), 2 species suggest dry forest at the site in the past (Pale-browed Tinamou [*Crypturellus transfasciatus*] and Crested Guan [*Penelope purpurascens*]). Also present at Talara in the late Pleistocene were large mammals characteristic of grassland, savanna, and dry forest, such as edentates (*Scelidodon*, *Holmesina*, *Eremotherium*), deer (*Odocoileus*, *Mazama*), proboscideans (*Stegomastodon*), dire wolves (*Canis dirus*), large jaguars (*Panthera onca* s.l.), and saber-toothed cats (*Smilodon fatalis*; Churcher 1959, Campbell 1979, Seymour 1983, Berta 1985). These findings led Lemon and Churcher (1961) and Campbell (1982) to propose that during the late Pleistocene the area near the site was predominantly grassland or savanna. Our results provide independent evidence to support this proposal, although the passerine fossils also argue for the

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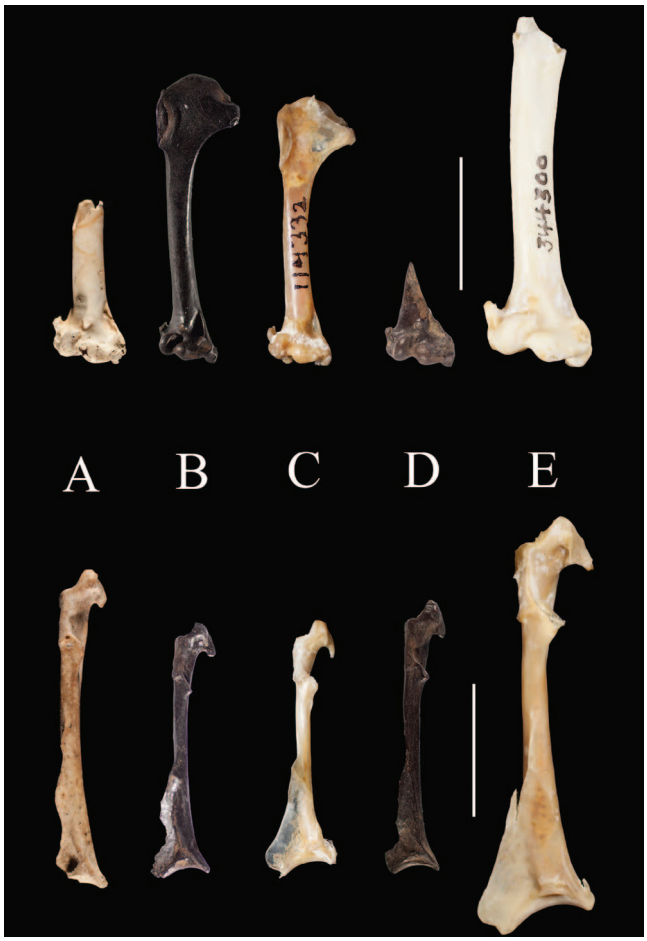


FIGURE 6. The humerus (above) and coracoid (below) of extinct and extant cowbird species. (**A**) *Pandanaris convexa* fossil (extinct; UF/PB 4221), Florida, USA. (**B**) *Molothrus bonariensis* fossil ROM 69963, Talara, Peru. (**C**) *Molothrus bonariensis* modern, LSUMZ 114332. (**D**) *Molothrus* nov. sp., fossil ROM 70030, Talara. (**E**) *Molothrus oryzivorus* modern, USNM (National Museum of Natural History) 344300. Scale bars = 10 mm.

past existence of dry forest and gallery forest. The late Pleistocene habitat matrix at or near the site probably did not include desert, which exists at Talara now.

The climatic mechanism(s) responsible for more mesic conditions and more diverse habitats at Talara during the late Pleistocene are unknown. On average, the Earth (including the tropics) was cooler and drier during glacial than interglacial intervals (Bush 1994, Peterson et al. 2000, Bromley et al. 2009). It is unlikely that meltwater from the Andes fueled the more mesic communities near Talara as there are few high peaks east of the site in the western Andean cordillera that would have sustained alpine glaciers during glacial intervals (Campbell 1979). Sea levels during the last glacial maximum (~25 to 18 ka) were ~120 m lower than they are today and reached modern levels by 6 ka (Clark et al. 2009). Given the steep continental shelf off the coast of Peru, the Pacific Ocean would have been only several tens of km farther from Talara during glacial times. Nevertheless, the lower sea levels and more distant coastline may have buffered Talara from the drying effects of the Humboldt Current during the late Pleistocene.

The Humboldt Current, found off the coast from southern Chile to northern Peru, fuels the nutrient-rich, cold upwelling that cools offshore air, which in turn causes the modern aridity of coastal Peru. Changes in trade winds and atmospheric pressure lead to a reduced temperature differential between the western and eastern Pacific Ocean that results in El Niño–Southern Oscillation (ENSO) events, which tend to occur on a 7–10 year cycle in modern times (Tudhope et al. 2001). During ENSO events, the upwelling ceases and surface waters warm, leading to a remarkable increase in precipitation that turns the desert of coastal northwestern Peru into an ephemeral shrubby grassland (Richter 2005, Muenchow et al. 2013). Perhaps longer-term, stronger, more frequent, or more persistent ENSO conditions resulted in the richer glacial-age floral and faunal communities in northwestern Peru in the past. It has been difficult, however, to reconstruct the periodicity and severity of ENSO events through time because different paleoclimate proxies yield different results. Sea surface temperature differentials have been stable since the Miocene (Zhang et al. 1998), which would have resulted in periodic ENSO cycles over the past 18 million years, although Wara et al. (2005) argue for permanent El Niño conditions during the Pliocene. Growth rings from corals in the western Pacific suggest that ENSO events have occurred since 130 ka, even during glacial periods, although the amplitude and duration of the events may have been more variable than in modern times (Zhang et al. 1998).

Icterids

At Talara, 296 of 625 (47%) of the passerine fossils are of icterids, with 3 of the 8 species being extinct. The fact that icterids are so common as late Pleistocene fossils may be due to their preference to form communal roosts near water (Oswald and Steadman 2011). These freshwater wetlands, whether more permanent lakes and marshes or more ephemeral ones lying on tar seeps after rains, would also serve as water sources for large mammals, thus augmenting their attractiveness to icterids. Four extinct species of Icteridae have been described from late Pleistocene sites in North America: *Euphagus magnirostris* (Miller 1929); *Pyelorhamphus molothroides* (Miller 1932); *Pandanaris convexa* (Miller 1947, Oswald and Steadman 2011); and *Cremaster tytthus* (Brodkorb 1959). The late Pleistocene extinctions of icterids included even very widespread species, such as *Pandanaris convexa* and *Euphagus magnirostris* (Oswald and Steadman 2011, Steadman et al. 2015). The losses were especially dramatic

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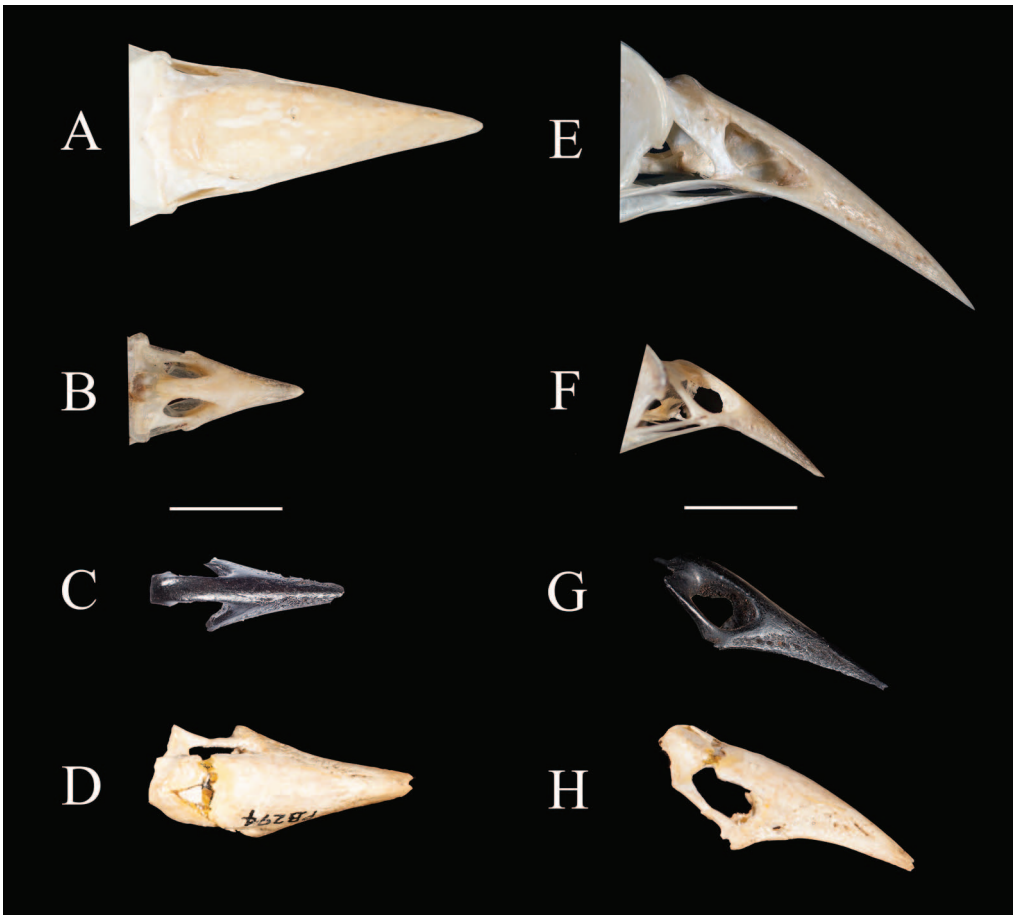


FIGURE 7. The rostrum of extinct and extant cowbirds in dorsal (**A**–**D**) and lateral (**E**–**H**) aspects. (**A**, **E**) *Molothrus oryzivorus* modern, USNM 344300. (**B, F**) *Molothrus bonariensis* modern, LSUMZ 114332. (**C**, **G**) *Molothrus* nov. sp., Talara fossil, ROM 70031. (**D**, **H**) *Pandanaris convexa* fossil, UF/PB 294. Scale bars = 10 mm.

among large-billed, cowbird-like forms such as *Pyelorhampus*, *Pandanaris*, *Molothrus* nov. sp., and perhaps *Cremaster*. The extinction of multiple species with a unifying morphological trait (a large bill) suggests the loss of foraging niches that existed across the Americas during the Pleistocene.

In addition, icterids are unique among New World passerines in that many species have commensal relationships with large mammals such as horses, cows, and bison (Lowther 1993, Martin 2002). In Africa, extant megamammals such as elephants and zebras are "ecosystem engineers" that help to maintain the savannas and grasslands upon which many bird species depend (Laws 1970); it is likely that Pleistocene megamammals played comparable roles in maintaining habitats favorable to icterids in the Americas (Steadman and Martin 1984, Oswald and Steadman 2011). While both climate change and human impacts fueled the Pleistocene-to-Holocene faunal changes in the region, the loss of biotic interactions also may have played a significant role for icterids when their large mammal associates were lost. All extant cowbird species also are brood parasites of other songbird species. The host of the large, extinct Pleistocene species of *Molothrus* at Talara may have been the now-extirpated Yellow-billed Cacique or the extinct species of troupial.

The modern distribution of *Euphagus* is restricted to North America; both extant species (Rusty Blackbird [*E. carolinus*] and Brewer's Blackbird [*E. cyanocephalus*]) are migratory. Therefore, the *E. magnirostris* fossils discovered in northwestern Peru (and in the Inciarte Tar Seeps in northwestern Venezuela; Steadman et al. 2015) may represent migratory individuals. Alternatively, perhaps especially if *E. magnirostris* was a megamammal commensal, this species may have had an extensive resident distribution in both North and South America, alongside the various edentates, artiodactyls, equids, and proboscideans that were lost at the end of the Pleistocene (Anderson 1984). The only modern resident passerine birds with ranges that extend from the southern United States into South America are the Vermilion Flycatcher

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FIGURE 8. The humerus (above) and coracoid (below) of troupial (*Icterus* spp.) taxa. (**A**) Talara fossil *Icterus icterus* s.l. humerus ROM 70056, coracoid ROM 70042. (**B**) Modern *Icterus icterus ridgwayi* (male, Colombia) UF 30896 (old PB catalogue number 20737). (**C**) Modern *Icterus croconotus strictifrons* (male, Bolivia) LSUMZ 126183. (**D**) Modern *Icterus croconotus croconotus* (female, Peru) LSUMZ 49015. Scale bars = 10 mm.

(*Pyrocephalus rubinus*; Farnsworth and Lebbin 2004) and Eastern Meadowlark (*Sturnella magna*; Fraga 2011a).

Nonanalog Bird Communities and Species' Responses to Change

Many Pleistocene biotic communities across the Americas are nonanalog compared with modern communities. In North America, for example, late Pleistocene rodent communities were composed of species that are allopatric today (Stafford et al. 1999, Blois et al. 2010, Semken et al. 2010). Pollen cores show that Andean plants once lived alongside tropical, lowland plant taxa in the Amazon Basin (Bush 1994, Colinvaux et al. 2000). Late Pleistocene nonanalog bird communities of the Americas reflect in part the loss of megafauna, which led to the loss of species or populations of large scavenging and predatory nonpasserine birds (vultures, condors, eagles, caracaras, etc.; Steadman and Martin 1984, Steadman et al. 2015). The nonanalog late Pleistocene passerine community that we discovered at Talara is what we might expect under a different climatic regime and with a very different community of large mammals. Considering that we could not radiocarbon-date the bird fossils themselves, we have no definitive evidence that all of the species identified in this study were contemporaneous. Nevertheless, in the late Quaternary sites with analog bird or mammal communities and a rigorous radiocarbon chronology, the time spans of the fossil deposits are measured in decades or at most a few centuries, rather than millennia (Stafford et al. 1999, Steadman et al. 2002, Semken et al. 2010). If the changing climatic conditions across the late Pleistocene to Holocene resulted in habitat changes and range shifts that led to high turnover of bird species composition at Talara, this suggests that biotic communities, whether birds or otherwise, may be continually in a state of flux, with the rate of change governed by the severity of the climatic (or anthropogenic) change. Because species have responded idiosyncratically to historical abiotic and biotic changes, the search for a single mechanism driving the changing diversity and distributions of tropical species may be futile.

Modern tropical dry forests in South America have a fragmented distribution in Andean valleys, on the Pacific slope of southwestern Ecuador and northwestern Peru (Tumbesian Region), and in a discontinuous ring around the Amazon Basin (Pennington et al. 2006, Särkinen et al. 2011). Very few species of bird are shared among these regions (Stotz et al. 1996). Our fossil evidence indicates that dry forest species had wider distributions in the past. The dearth of shared species among modern dry forest communities might reflect, in part, population extirpation since the last ice age. This hypothesis can be tested through more paleontological research.

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LITERATURE CITED

Absy, M. L., A. F. Cleef, M. Fournier, L. Martin, M. Servant, A. Sfeddine, M. F. Ferreira da Silva, F. Soubies, K. Suguio, B. Turcq, and T. van der Hammen (1991). Mise en évidence de quatre phases d'ouverture de la forêt dense de sudest de l'Amazonie au cours des 60.000 dernières anneés. Comptes Rendus Academie des Sciences, Paris, Series II 312:673–678.

Anderson, E. (1984). Who's who in the Pleistocene: A mammalian bestiary. In Quaternary Extinctions (P. S. Martin and R. G. Klein, Editors). The University of Arizona Press, Tucson, AZ, USA. pp. 40–89.

Baumel, J. J., A. S. King, A. M. Lukas, J. E. Breazile, and H. E. Evans (Editors) (1993). Nomina Anatomica Avium. Academic Press, London, UK.

Berta, A. (1985). The status of *Smilodon* in North and South America. Contributions in Science, Natural History Museum of Los Angeles County 370:1–14.

Blois, J. L., J. L. McGuire, and E. A. Hadly (2010). Small mammal diversity loss in response to late-Pleistocene climatic change. Nature 465:771–775.

Brodkorb, P. (1959). The Pleistocene avifauna of Arredondo, Florida. Bulletin of the Florida State Museum of Biological Sciences 4:269–291.

Bromley, G. R. M., J. M. Schaefer, G. Winckler, B. L. Hall, C. E. Todd, and K. M. Rademaker (2009). Relative timing of last glacial maximum and late-glacial events in the central tropical Andes. Quaternary Science Reviews 28:2514–2526.

Brumfield, R. (2012). Inferring the origins of lowland Neotropical birds. The Auk 129:367–376.

Bush, M. B. (1994). Amazonian speciation: A necessarily complex model. Journal of Biogeography 21:5–17.

Campbell, K. E., Jr. (1976). The late Pleistocene avifauna of La Carolina, southwestern Ecuador. In Collected Papers in Avian Paleontology Honoring the 90th Birthday of Alexander Wetmore (S. L. Olson, Editor). Smithsonian Contributions to Paleobiology 27:155–168.

Campbell, K. E., Jr. (1979). The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. Royal Ontario Museum Life Sciences Contributions 118:1–203.

Campbell, K. E., Jr. (1982). Late Pleistocene events along the coastal plain of northwestern Peru. In Biological Diversity in the Tropics (G. Prance, Editor). Columbia University Press, New York, NY, USA. pp. 423–440.

Churcher, C. S. (1959). Fossil *Canis* from the tar pits of La Brea, Peru. Science 130:564–565.

Churcher, C. S. (1966). The insect fauna from the Talara Tar Seeps, Peru. Canadian Journal of Zoology 44:985–993.

Clark, P. U., A. S. Dyke, J. D. Shakun, A. E. Carlson, J. Clark, B. Wohlfarth, J. X. Mitrovica, S. W. Hostetler, and A. M. McCabe (2009). The last glacial maximum. Science 325:710–714.

Cohen, K. M., and P. Gibbard (2011). Global Chronostratigraphical Correlation Table for the Last 2.7 Million Years. International Commission on Stratigraphy Subcommission on Quaternary Stratigraphy, Cambridge, UK.

Colinvaux, P. A., and P. E. Oliveira (2001). Amazon plant diversity and climate through the Cenozoic. Palaeogeography, Palaeoclimatology, Palaeoecology 166:51–63.

Colinvaux, P. A., M. B. Bush, M. I. Steinitz-Kannan, and M. C. Mille (1997). Glacial and postglacial records from the Ecuadorian Andes and Amazon. Quaternary Research 48:69–78.

Colinvaux, P. A., K.-B. Liu, P. Oliveira, M. B. Bush, M. C. Miller, and M. Steinitz-Kannan (1996a). Temperature depression in the lowland tropics in glacial times. Climatic Change 32:19–33.

Colinvaux, P. A., P. E. Oliveira, and M. B. Bush (2000). Amazonian and Neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. Quaternary Science Reviews 19:141–169.

Colinvaux, P. A., P. E. Oliveira, J. E. Moreno, M. C. Miller, and M. B. Bush (1996b). A long pollen record from lowland Amazonia forest and cooling in glacial times. Science 274:85–87.

Farnsworth, A., and D. Lebbin (2004). Vermilion Flycatcher (*Pyrocephalus rubinus*). In Handbook of the Birds of the World Alive, (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http//www.hbw.com/node/57383

Fraga, R. (2011a). Eastern Meadowlark (*Sturnella magna*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http//www.hbw.com/node/62330

Fraga, R. (2011b). Yellow-billed Cacique (*Amblycercus holosericeus*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http://www.hbw.com/node/62221

Friscia, A. R., B. Van Valkenburg, L. Spencer, and J. Harris (2008). Chronology and spatial distribution of large mammal bones in PIT 91, Rancho La Brea. Palaios 23:35–42.

Gold, D. A., J. Robinson, A. B. Farrell, J. M. Harris, O. Thalmann, and D. K. Jacobs (2014). Attempted DNA extraction from a Rancho La Brea Columbian mammoth (*Mammuthus columbi*): Prospects for ancient DNA from asphalt deposits. Ecology and Evolution 4:329–336.

Graham, A. (1999). The Andes: A geological overview from a biological perspective. Annals of the Missouri Botanical Garden 96:371–385.

Grant, B. R. (1985). Selection on bill characters in a population of Darwin's Finches *Geospiza conirostris* on Isla Genovesa, Galapagos. Evolution 39:523–532.

Haffer, J. (1969). Speciation in Amazonian forest birds. Science 165:131–137.

Hamon, J. H. (1964). Osteology and Paleontology of the Passerine Birds of the Reddick, Florida, Pleistocene. Florida Geological Survey Geological Bulletin No. 44, Florida Geological Survey, Tallahassee, FL, USA.

Heaton, T. J., P. G. Blackwell, and C. E. Buck (2009). A Bayesian approach to the estimation of radiocarbon calibration curves: The INTCAL09 methodology. Radiocarbon 51:1151–1164.

Hoorn, C., F. P. Wesselingh, H. ter Steege, M. A. Bermudez, A. Mora, J. Sevink, I. Sanmartin, A. Sanchez-Meseguer, C. L. Anderson, J. P. Figueiredo, C. Jaramillo, et al. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330:927–931.

Downloaded From: https://bioone.org/journals/The-Auk on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Howard, H. (1929). The avifauna of Emeryville Shellmound. University of California Publications in Zoology 32:301–394.

Janzen, D. (1988). Tropical dry forest: The most endangered tropical ecosystem. In Biodiversity (E. Wilson, Editor). National Academy Press, Washington, DC, USA. pp. 130–137.

Jaramillo, A. (2011). Parrot-billed Seedeater (*Sporophila peruviana*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain. http//www.hbw.com/node/62124

Jaramillo, A., and P. Burke (1999). New World Blackbirds: The Icterids. Princeton University Press, Princeton, NJ, USA.

Laws, R. M. (1970). Elephants as agents of habitat and landscape change in East Africa. Oikos 21:1–15.

Lemon, R. H., and C. S. Churcher (1961). Pleistocene geology and paleontology of the Talara Region, northwest Peru. American Journal of Science 259:410–429.

Lowther, P. E. (1993). Brown-headed Cowbird (*Molothrus ater*). In The Birds of North America Online (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.47

Martin, S. G. (2002). Brewer's Blackbird (*Euphagus cyanocephalus*). In The Birds of North America Online (A. Pool, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.616

Miller, A. H. (1929). The passerine remains from Rancho La Brea in the paleontological collections of the University of California. University of California Publications, Bulletin of the Department of Geological Sciences 19:1–22.

Miller, A. H. (1932). An extinct icterid from Shelter Cave, New Mexico. The Auk 49:38–41.

Miller, A. H. (1947). A new genus of icterid. The Condor 49:22–24.

Muenchow, J., H. von Wehrden, E. F. Rodríguez, R. Arisméndiz Rodríguez, F. Bayer, and M. Richter (2013). Woody vegetation of a Peruvian tropical dry forest along a climatic gradient depends more on soil than annual precipitation. Erdkunde 67:241–248.

Oswald, J. A., and D. W. Steadman (2011). Late Pleistocene birds of Sonora, Mexico. Palaeogeography, Palaeoclimatology, Palaeoecology 301:56–63.

Parker, T. A., III, T. S. Schulenberg, M. Kessler, and W. H. Wust (1995). Natural history and conservation of the endemic avifauna in north-west Peru. Bird Conservation International 5:201–231.

Pennington, R. T., D. E. Prado, and C. A. Pendry (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27:261–273.

Pennington, R. T., J. A. Ratter, and G. P. Lewis (2006). An overview of the plant diversity, biogeography and conservation of Neotropical savannas and seasonally dry forests. In Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography, and Conservation (R. T. Pennington, G. P. Lewis, and J. A. Ratter, Editors). CRC Press, Boca Raton, FL, USA. pp. 1–29.

Peterson, L. C., G. H. Haug, K. A. Hughen, and U. Röhl (2000). Rapid changes in the hydrologic cycle of the tropical Atlantic during the last glacial. Science 290:1947–1951.

Prado, D. E., and P. E. Gibbs (1993). Patterns of species distributions in the dry seasonal forests of South America. Annals of the Missouri Botanical Garden 80:902–927.

Reimer, P. J., M. G. L. Baillie, E. Bard, A. Bayliss, J. W. Beck, P. G. Blackwell, C. Bronk Ramsey, C. E. Buck, G. S. Burr, R. L. Edwards, M. Friedrich, et al. (2009). IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. Radiocarbon 51:1111–1150.

Remsen, J. V., Jr., C. D. Cadena, A, Jaramillo, A. M. Nores, J. F. Pacheco, J. Pérez-Emán, M. B. Robbins, F. G. Stiles, D. F. Stotz, and K. J. Zimmer (2014). A classification of the bird species of South America. South American Classification Committee, American Ornithologists' Union. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm

Ribas, C. C., A. Aleixo, A. C. R. Nogueira, C. Y. Miyaki, and J. Cracraft (2012). A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. Proceedings of the Royal Society of London, Series B 279:681–689.

Richardson, J. B., III (1978). Early man on the Peruvian North Coast: Early maritime exploitation and the Pleistocene and Holocene environment. In Early Man in America from a Circum-Pacific Perspective (A. Bryan, Editor). University of Alberta Press, Edmonton, AB, Canada. pp. 274–289.

Richter, M. (2005). Vegetation development before, during, and after El Niño 1997/98 in northwestern Peru. Lyonia 8:19–27.

Ridgely, R. S., and G. Tudor (2009). Field Guide to the Songbirds of South America: The Passerines. University of Texas Press, Austin, TX, USA.

Rull, V. (2011). Neotropical biodiversity timing and potential drivers. Trends in Ecology & Evolution 26:508–513.

Sandweiss, D. H. (2003). Terminal Pleistocene through mid-Holocene: Archaeological sites as paleoclimatic archives for the Peruvian coast. Palaeogeography, Palaeoclimatology, Palaeoecology 194:23–40.

Särkinen, T., J. R. V. Iganci, R. Linares-Palomino, M. F. Simon, and D. E. Prado (2011). Forgotten forests—Issues and prospects in biome mapping using seasonally dry tropical forests as a case study. BMC Ecology 11:27. doi:10.1186/1472-6785-11-27

Schulenberg, T. S., D. F. Stotz, D. F. Lane, J. P. O'Neill, and T. A. Parker, III (2007). Birds of Peru. Princeton University Press, Princeton, NJ, USA.

Semken, H. A., Jr., R. W. Graham, and T. W. Stafford, Jr. (2010). AMS ^{14}C analysis of late Pleistocene non-analog faunal components from 21 cave deposits in southeastern North America. Quaternary International 217:240–255.

Seymour, K. L. (1983). The Felinae (Mammalia, Felidae) from the late Pleistocene tar pits at Talara, Peru, with a critical examination of the fossil and recent felines of North and South America. M.S. thesis, University of Toronto, Toronto, ON, Canada.

Shaw, C. A., and J. P Quinn (1986). Rancho La Brea: A look at coastal southern California's past. California Geology 29:123–133.

Smith, B. T., A. Amei, and J. Klicka (2012). Evaluating the role of contracting and expanding rainforest in initiating cycles of speciation across the Isthmus of Panama. Proceedings of the Royal Society of London, Series B 279:3520–3526.

Stafford, T. W., Jr., H. A. Semken, Jr., R. W. Graham, W. F. Klippel, A. Markova, N. G. Smirnov, and J. Southon (1999). First accelerator mass spectrometry ^{14}C dates documenting contemporaneity of nonanalog species in late Pleistocene mammal communities. Geology 27:903–906.

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Steadman, D. W. (1982). The origin of Darwin's finches (Fringillidae, Passeriformes). Transactions of the San Diego Society of Natural History 19:279–296.

Steadman, D. W., and P. S. Martin (1984). Extinction of birds in the late Pleistocene of North America. In Quaternary Extinctions (P. S. Martin and R. G. Klein, Editors). University of Arizona Press, Tucson, AZ, USA. pp. 466–477.

Steadman, D. W., and M. C. McKitrick (1982). A Pliocene bunting from Chihuahua, México. The Condor 84:240–241.

Steadman, D. W., and J. I. Mead (2010). A late Pleistocene bird community at the northern edge of the tropics in Sonora, Mexico. American Midland Naturalist 163:423–441.

Steadman, D. W., J. Arroyo-Cabrales, E. Johnson, and A. F. Guzman (1994). New information on the late Pleistocene birds from San Josecito Cave, Nuevo León, México. The Condor 96:577–589.

Steadman, D. W., J. A. Oswald, and A. D. Rincón (2015). The diversity and biogeography of late Pleistocene birds from the lowland Neotropics. Quaternary Research 83:555–564.

Steadman, D. W., G. K. Pregill, and D. V. Burley (2002). Rapid prehistoric extinction of birds and iguanas in Polynesia. Proceedings of the National Academy of Sciences USA 99: 3673–3677.

Stotz, D. F., J. W. Fitzpatrick, T. A Parker, III, and D. K. Moskovits (1996). Neotropical Birds: Ecology and Conservation. University of Chicago Press, Chicago, IL, USA.

Tudhope, A. W., C. P. Chilcott, M. T. McCulloch, E. R. Cook, J. Chappell, R. M. Ellam, D. W. Lea, J. M. Lough, and G. B. Shimmield (2001). Variability in the El Niño-Southern Oscillation through a glacial-interglacial cycle. Science 291: 1511–1516.

van der Hammen, T. (1972). Changes in vegetation and climate in the Amazon Basin and surrounding areas during the Pleistocene. Geologie en Mijnbouw 51:641–643.

Wara, M. W., A. C. Ravelo, and M. L. Delaney (2005). Permanent El Niño-like conditions during the Pliocene warm period. Science 309:758–761.

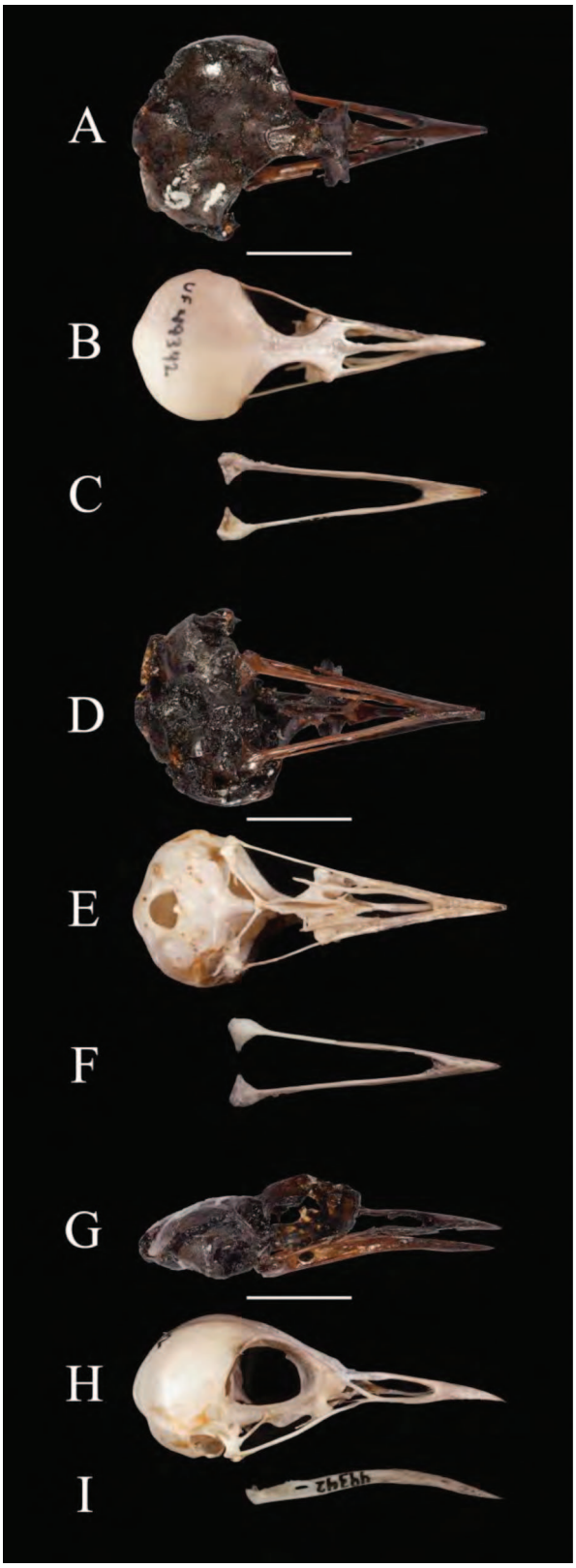
Werneck, F. P., T. Gamble, G. R. Colli, M. T. Rodrigues, and J. W. Sites, Jr. (2012). Deep diversification and long-term persistence in the South American 'dry diagonal': Integrating continent-wide phylogeography and distribution modeling of geckos. Evolution 66:3014–3034.

Zhang, R. H., L. M. Rothstein, and A. J. Busalacchi (1998). Origin of upper-ocean warming and El Niño change on decadal scales in the tropical Pacific Ocean. Nature 391: 879–883.

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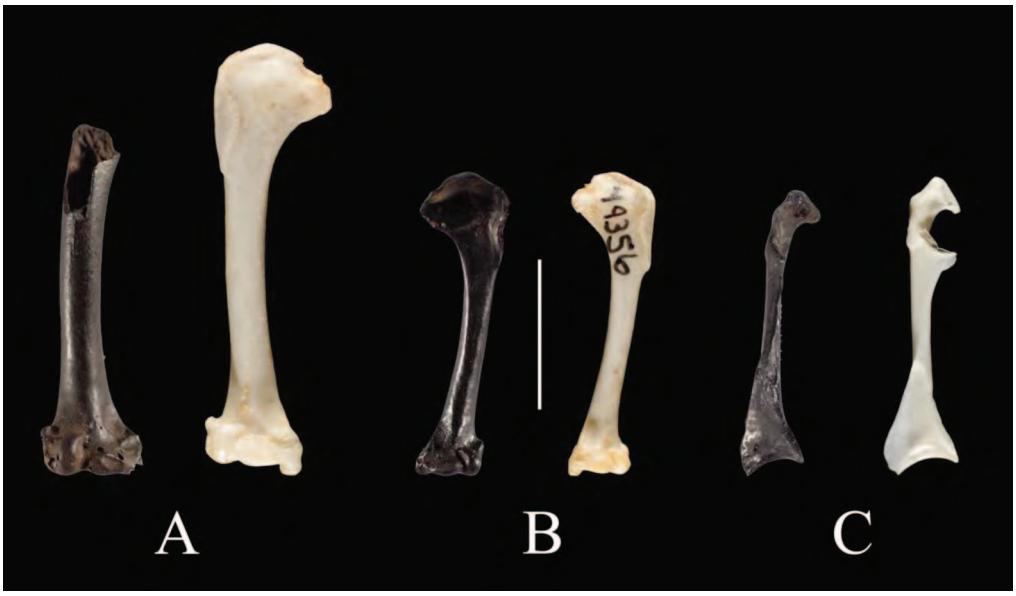
APPENDIX. COMPARATIVE OSTEOLOGY

Osteological characters used to identify the Talara Tar Seep, Peru, passerine fossils. Royal Ontario Museum (ROM) catalog numbers for each identified fossil are found in Supplemental Material Table S12. All characters were scored relative to the character state of the reference skeletons. All specimens at table column headings are male unless otherwise noted, although female specimens (if available) also were included in osteological comparisons. Comparisons included more than 1 specimen (typically 5 to 8) per species. At the level of family or genus, a few of these characters are modified from those in Hamon (1964).



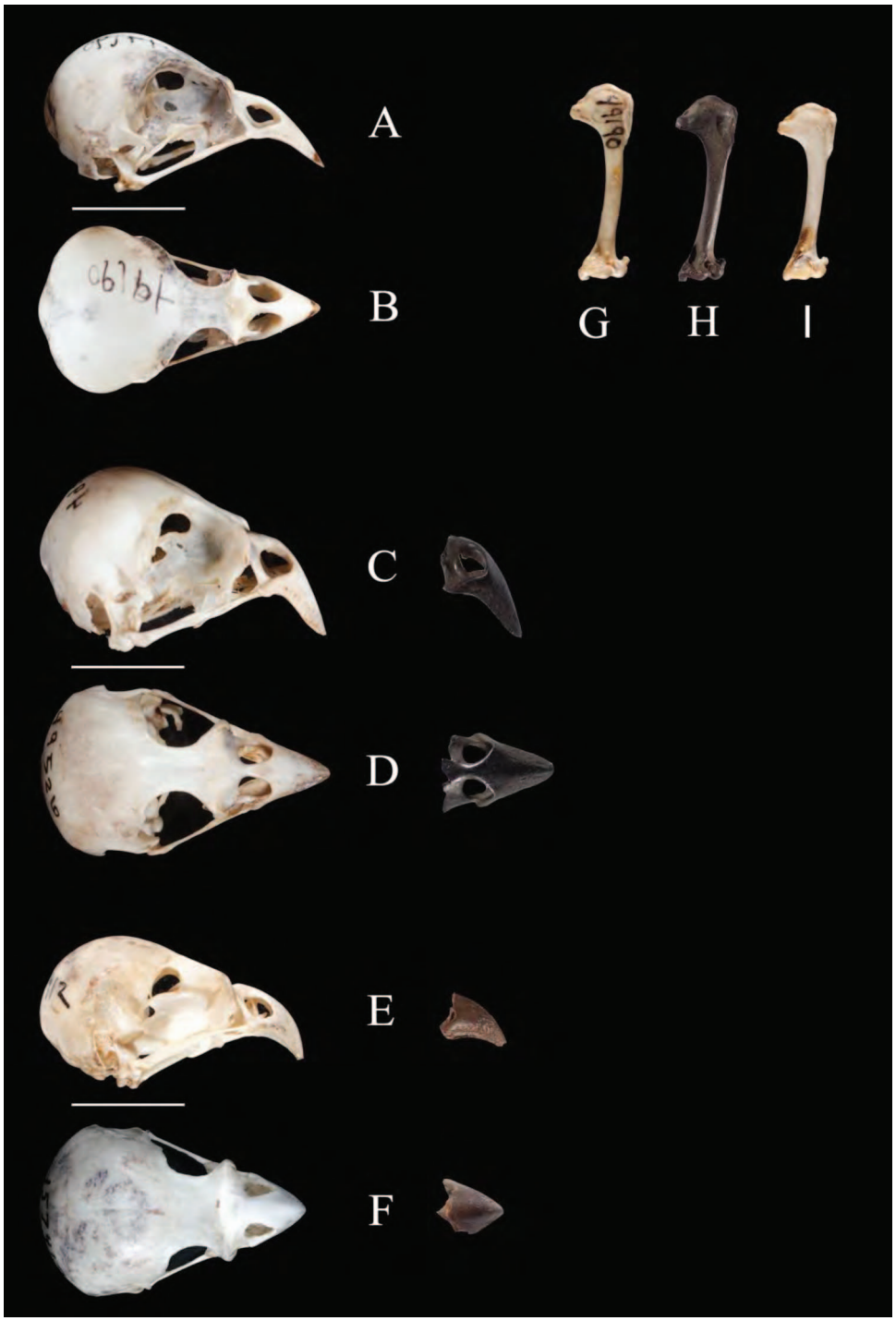
APPENDIX FIGURE 3. Skulls and mandibles of *Melanopareia elegans*. The fossil (ROM 69700; **A**, **D**, **G**) has the cranium and mandible still articulated. The modern (UF 49342) cranium (**B, E, H**) and mandible (**C, F, I)** are shown below the fossil in different aspects (**A**–**C**, cranial; **D**–**F**, ventral; **G**–**I**, lateral). Scale bars = 10 mm.

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APPENDIX FIGURE 4. Postcranial elements of suboscines. For each pair, fossils are on the left, modern specimens on the right. (**A**) Fossil (ROM 69707) and modern (UF 49489) humerus of *Myiodynastes bairdii*. (**B**) Fossil (ROM 69701) and modern (UF 49356) humerus of *Thamnophilus bernardi*. (**C**) Fossil (ROM 69705) and modern coracoid of *Myiozetetes similis* (modern: *M. s. columbianus*, UF 46254). The fossil is likely *M. s. grandis* (see Appendix Table 10). Scale bar = 10 mm.

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APPENDIX FIGURE 9. Rostra and humeri of seedeaters. (**A**, **B**) *Sicalis flaveola* (UF 49190) in lateral and dorsal aspects. (**C**, **D**) *Sicalis taczanowskii* in lateral and dorsal aspects, with modern specimen (UF 49526) on left and fossil (ROM 69904) on right. (**E**, **F**) *Sporophila peruviana* in lateral and dorsal aspects, with modern specimen (LSUMZ 157412) on left and fossil (ROM 69926) on right. Humeri (**G**–**I**) of *Sicalis* species. (**G**) *Sicalis flaveola* modern, UF 49190. (**H**) *Sicalis* sp. fossil, Talara, ROM 69792. (**I**) *Sicalis taczanowskii* modern, UF 49526. Scale bars = 10 mm.

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APPENDIX TABLE 2. Osteological characters used to identify species of Icteridae of similar size and osteology. See Tables 3–5 for *Icterus* and *Euphagus* characters.

Element	Character	LSUMZ 157416, *Dives warszewiczi*	UF 33277, *Amblycercus holosericeus*	LSUMZ 114332, *Molothrus bonariensis*	ROM 70030, Fossil: *Molothrus* nov. sp.	UF 49374, *Sturnella bellicosa*
Humerus	Length of the ectepicondylar prominence	long	short	long	short	long
	Shape of the curvature of the ectepicondylar prominence away from the shaft	intermediate	wide	narrow	intermediate	intermediate
	Depth of the curvature, ectepicondylar prominence	deep	shallow	deep	shallow	deep
	Symmetry of the curvature of the ectepicondylar prominence away from the shaft	asymmetrical	symmetrical	symmetrical	symmetrical	symmetrical
	Extension of the external tricipital groove visible in the palmar view (1: visible; 0: not visible; 0.5: partially visible)	0	1	0	0	0
	Length and width of the additional process on the ectepicondylar prominence	short, wide	long, narrow	short, wide	short, wide	intermediate, wide
	Shape of the attachment of the pronator brevis	rounded	"D" shaped	"D" shaped	"D" shaped	"D" shaped
	Depth of the attachment of the pronator brevis	Intermediate–deep	deep	deep	deep	deep
	Depth of the attachment of the pronator brevis	Intermediate–deep	deep	deep	deep	deep
	Curvature of the bicipital surface away from the shaft	slight curve	slight curve	slight curve	N/A	curved
	Presence of continuous bicipital crest	complete	incomplete	incomplete	N/A	incomplete
	Shape of internal tuberosity	robust ridge	ridge not present	ridge not present	N/A	ridge present

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APPENDIX TABLE 2. Continued.

Element	Character	LSUMZ 157416, *Dives warszewiczi*	UF 33277, *Amblycercus holosericeus*	LSUMZ 114332, *Molothrus bonariensis*	ROM 70021–70029, Fossil: *Molothrus* nov. sp.	UF 49374, *Sturnella bellicosa*
Coracoid	Depth of the curvature of the brachial tuberosity away from the shaft	intermediate	deep	deep	very shallow	intermediate
	Shape of tip of the brachial tuberosity	intermediate width, rounded	intermediate width, hooked	long, pointed	wide, rounded with slight hook	intermediate width, rounded
	Shape of curvature of the brachial tuberosity away from the shaft	wide	wide	narrow	very narrow	narrow
	Length of brachial tuberosity	long	long	long	short	intermediate
	Shape of the procoracoid	rounded	rounded	intermediate	pointed	pointed
	Length of procoracoid (measured from shaft)	short	short	long	long	long
		LSUMZ 157416, *Dives warszewiczi*	UF 33277, *Amblycercus holosericeus*	LSUMZ 114332, *Molothrus bonariensis*	ROM 70104, Fossil: *Molothrus* nov. sp.	UF 47467, *Sturnella bellicosa*
Rostrum	Shape of narial bar	intermediate, squared	wide, squared	slight taper, squared	N/A	intermediate, squared
	Narial bar (mm, male)	1.97	4.30	1.68	2.26–2.52 (range; likely dimorphic)	
	Narial bar (mm, female)	1.80	3.54	N/A		2.26
Mandible tip	Posterior margin of mandibular symphysis in dorsal–lateral aspect	intermediate	thin	thick	N/A	intermediate
	Width and depth of medial ventral trough	narrow, intermediate	wide, deep	wide, deep	N/A	intermediate, deep
	Length of retroarticular process	short	very long	absent	N/A	long
	Shape of mandibular fenestra	ellipse	squared ellipse	ellipse	N/A	ellipse
	Shape and depth of the angle of the mandibular symphysis in lateral aspect	rounded, shallow	angled, deep	rounded, deep	N/A	rounded, shallow

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APPENDIX TABLE 3. *Icterus* cranial characters referenced when identifying cranial elements preserved as fossils. All characters were scored relative to the character state of the elements considered. All specimens are male unless denoted by an "*" indicating that they are female. Note: No fossil cranial material from Talara was identified as belonging to *Icterus*. This table is included in the Appendix as a reference to the characters scored for comparably sized species of icterids in Table 2.

Element	Character	LSUMZ 126183, *Icterus croconotus croconotus* (Bolivia)	LSUMZ 49015,* *Icterus croconotus croconotus* (Peru)	UF 30896, *Icterus icterus ridgwayi*	UF 49305, *Icterus graceannae*	UF 49200,* *Icterus mesomelas*
Rostrum	Shape of narial bar	slight taper, squared	slight taper, squared	narrow, squared	slight taper, squared	narrow, squared
	Narial bar (mm, male)	1.55	N/A	1.84 UF 30890	1.88	
	Narial bar (mm, female)		1.38	1.61		1.15
Mandible tip	Posterior margin of mandibular symphysis in dorsal–lateral aspect	thin	thin	thin	thin	thin
	Width and depth of medial ventral trough	narrow, intermediate	intermediate, shallow	narrow, shallow	wide, shallow	intermediate, intermediate
	Length of retroarticular process	long	long	long	long	long
	Shape of mandibular fenestra	more rounded relative to other *Icterus icterus* forms	ellipse	ellipse	ellipse	round
	Shape and depth of the angle of the mandibular symphysis in lateral aspect	angled, deep	angled, deep	angled, deep	angled, deep	intermediate, deep

APPENDIX TABLE 4. Osteological characters used to identify postcranial elements of *Icterus*. All characters were scored relative to the character state of the modern specimens. All specimens are male unless denoted by an "*" indicating that they are female.

Element	Character	ROM 70056–70064, Fossil: *Icterus icterus*	LSUMZ 126183, *Icterus croconotus croconotus* (Bolivia)	LSUMZ 49015,* *Icterus croconotus croconotus* (Peru)	UF 30896, *Icterus icterus ridgwayi*	UF 49305, *Icterus graceannae*	UF 49200,* *Icterus mesomelas*
Humerus	Length of the ectepicondylar prominence	intermediate	long	long	intermediate	long	long
	Shape of the curvature of the ectepicondylar prominence away from the shaft	intermediate	wide	wide	wide	narrow	narrow
	Depth of the curvature of the ectepicondylar prominence	deep	deep	deep	shallow	intermediate	intermediate

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APPENDIX TABLE 4. Continued.

Element	Character	ROM 70056–70064, Fossil: *Icterus icterus*	LSUMZ 126183, *Icterus croconotus croconotus* (Bolivia)	LSUMZ 49015,* *Icterus croconotus croconotus* (Peru)	UF 30896, *Icterus icterus ridgwayi*	UF 49305, *Icterus graceannae*	UF 49200,* *Icterus mesomelas*
	Symmetry of the curvature of the ectepicondylar prominence away from the shaft	asymmetrical	symmetrical	symmetrical	symmetrical	symmetrical	asymmetrical
	Extension of the external tricipital groove visible in the palmar view (1: visible; 0: not visible; 0.5: partially visible)	0	1	1	1	0	0
	Length and width of the additional process on ectepicondylar prominence	very short	intermediate, wide	intermediate, wide	very short, very wide	very short, wide	short, very wide
	Shape of the attachment of the pronator brevis	rounded	rounded	rounded	rounded	rounded	"D" shaped
	Depth of the attachment of the pronator brevis	deep	intermediate	deep	intermediate	deep	deep
	Curvature of the bicipital surface away from the shaft	curved	curved	curved	curved	curved	curved
	Presence of continuous bicipital crest	complete	complete	complete	complete	incomplete	incomplete
	Shape of internal tuberosity	ridge present	ridge present	ridge present	ridge present	ridge present	ridge present

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APPENDIX TABLE 4. Continued.

Element	Character	ROM 70042–70055, Fossil: *Icterus icterus*	LSUMZ 126183, *Icterus croconotus croconotus* (Bolivia)	LSUMZ 49015,* *Icterus croconotus croconotus* (Peru)	UF 30896, *Icterus icterus ridgwayi*	UF 49305, *Icterus graceannae*	UF 49200,* *Icterus mesomelas*
Coracoid	Depth of the curvature of the brachial tuberosity away from the shaft	shallow	intermediate	shallow	shallow	shallow	deep
	Shape of the tip of the brachial tuberosity	intermediate width, hooked	intermediate width, rounded	wide, hooked	narrow, hooked	wide	narrow, hooked
	Shape of curvature of the brachial tuberosity away from the shaft	wide	intermediate	wide	wide	wide	wide
	Length of brachial tuberosity	intermediate	long	short	long	short	long
	Shape of the procoracoid	pointed	pointed	intermediate	pointed	rounded	rounded
	Length of procoracoid (measured from shaft)	long	short	short	long	intermediate	long

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APPENDIX TABLE 5. Characters used to identify fossils in the genus *Euphagus*.

Element	Character	UF 31110, *Euphagus carolinus*	UF 31114, *Euphagus cyanocephalus*	ROM 70107–70113, Fossil: *Euphagus* cf. *magnirostris*
Humerus	Length of the ectepicondylar prominence	long	intermediate	short
	Shape of the curvature of the ectepicondylar prominence away from the shaft	intermediate	wide	narrow
	Depth of the curvature of the ectepicondylar prominence	deep	shallow	shallow
	Symmetry of the curvature of the ectepicondylar prominence away from the shaft	symmetrical	symmetrical	asymmetrical
	Extension of the external tricipital groove visible in the palmar view (1: visible; 0: not visible; 0.5: partially visible)	0	0	0
	Length and width of the additional process on ectepicondylar prominence	very short, very wide	short, very wide	very short, very wide
	Shape of the attachment of the pronator brevis	rounded	"D" shaped	"D" shaped
	Depth of the attachment of the pronator brevis	intermediate	shallow	deep
	Curvature of the bicipital surface away from the shaft	curved	slight curve	N/A
	Presence of continuous bicipital crest	incomplete	nearly complete	N/A
	Shape of internal tuberosity	ridge present	ridge present	N/A
		UF 31110, *Euphagus carolinus*	UF 31114, *Euphagus cyanocephalus*	ROM 70114–70139, Fossil: *Euphagus* cf. *magnirostris*
Coracoid	Depth of the curvature of the brachial tuberosity away from the shaft	shallow	shallow	shallow
	Shape of the tip of the brachial tuberosity	intermediate width, hooked	wide, slightly hooked	wide, hooked
	Shape of the curvature of the brachial tuberosity away from the shaft	wide	wide	wide
	Length of brachial tuberosity	intermediate	short	short
	Shape of the procoracoid	intermediate	intermediate	pointed
	Length of procoracoid (measured from shaft)	long	long	long
		UF 31110, *Euphagus carolinus*	UF 31114, *Euphagus cyanocephalus*	ROM 70104–70106, Fossil: *Euphagus* cf. *magnirostris*
Rostrum	Shape of narial bar	narrow, hourglass	narrow, hourglass	N/A
	Narial bar (mm, male)	1.18	1.20	N/A
	Narial bar (mm, female)	1.07	1.18	N/A
Mandible tip	Posterior margin of mandibular symphysis in dorsal–lateral aspect	intermediate–thin	intermediate	missing
	Width and depth of medial ventral trough	narrow, intermediate	narrow, intermediate	N/A
	Length of retroarticular process	absent	absent	N/A
	Shape of mandibular fenestra	elongated ellipse	elongated ellipse	N/A
	Shape and depth of the angle of the mandibular symphysis in lateral aspect	rounded, intermediate	rounded, intermediate	missing

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APPENDIX TABLE 6. Osteological characters used to identify "seedeater" (Thraupidae) fossils. Referenced Talara fossil material: ROM catalog numbers 69791–69929.

Element	Character	UF 49526, *Sicalis taczanowskii*	UF 49190, *Sicalis flaveola*	LSUMZ 157412, *Sporophila peruviana*	UF 49371, *Rhynchospiza stolzmanni*	LSUMZ 157397, *Piezorina cinerea*
Humerus (distal)	Length of the ectepicondylar prominence	long	long	short	intermediate	long
	Shape of the curvature of the ectepicondylar prominence away from the shaft	rounded	rounded	rounded	rounded	rounded
	Depth of the curvature of the ectepicondylar prominence	deep	deep	shallow	intermediate	deep
	Symmetry of the curvature of the ectepicondylar prominence away from the shaft	symmetrical	symmetrical	symmetrical	symmetrical	symmetrical
	Shape of the attachment of the pronator brevis	"D" shaped	"D" shaped	"D" shaped	rounded	"D" shaped
	Depth of the attachment of the pronator brevis	deep	deep	deep	intermediate	deep
	Curvature of rostrum in lateral aspect	deeply angled	rounded, gentle curve	rounded, gentle curve	rounded, gentle curve	gentle slope
Rostrum	Shape of narial bar	hourglass	hourglass	very thick, hourglass	rectangular	thick, hourglass
	Narial bar (mm, male)	1.41	1.22	2.32	1.63	2.72
	Shape of os nares	circular	noncircular	circular	circular	noncircular
	Shape of mandibular fenestra	medium ellipse	large ellipse	tear shaped	pill shaped	ellipse
Mandible	Shape and depth of the angle of the mandible (where the intermediate part of the mandible attaches to the symphyseal part) in lateral aspect	rounded, deep	elliptical, deep	angled, deep	rounded square, intermediate	rounded point
	Length of the intermediate part of the ramus	short	long	intermediate	intermediate	long

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APPENDIX TABLE 7. Osteological characters used to identify martin (Hirundinidae) fossils.

Element	Character	UF 27837, *Progne tapera*	UF 27853, *Progne chalybea*	ROM 69708–69710, Fossils: *Progne* sp.
Humerus	Length of the ectepicondylar prominence	long	intermediate	long
	Shape of the curvature of the ectepicondylar prominence away from the shaft	rounded, intermediate	rounded, narrow	round, intermediate
	Depth of the curvature of the ectepicondylar prominence	deep	intermediate	intermediate
	Symmetry of the curvature of the ectepicondylar prominence away from the shaft	symmetrical	symmetrical	symmetrical
	Extension of the external tricipital groove visible in the palmar view	none	none	none
	Shape of the additional process on ectepicondylar prominence	absent	rounded, minute	absent
	Shape of the attachment of the pronator brevis	rounded	"D" shaped	rounded
	Depth of the attachment of the pronator brevis	shallow	intermediate	intermediate

Element	Character			ROM 69711–69712, Fossils: *Progne* sp.
Coracoid	Depth of the curvature of the brachial tuberosity away from the shaft	shallow	intermediate	intermediate
	Shape of the tip of the brachial tuberosity	rounded, wide	squared, wide	squared, wide
	Shape of curvature of the brachial tuberosity away from the shaft	very wide	wide	wide
	Length of brachial tuberosity	short	short	intermediate
	Shape of the procoracoid	rounded, long	rounded, long	rounded, long
	Length of procoracoid (measured from shaft)	shallow	shallow	very shallow

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APPENDIX TABLE 8. Osteological characters used to identify swallow (Hirundinidae) fossils.

Element	Character	ROM 69713–69715, Fossil: *Tachycineta stolzmanni*	LSUMZ 90118, *Tachycineta stolzmanni* (Sex = U)	UF 27878, *Tachycineta bicolor*
Humerus	Length of the ectepicondylar prominence	short–intermediate	short–intermediate	long
	Shape of the curvature of the ectepicondylar prominence away the from shaft	rounded, intermediate	rounded, intermediate	rounded, wide
	Depth of the curvature of the ectepicondylar prominence	shallow	shallow	intermediate
	Symmetry of the curvature of the ectepicondylar prominence away from the shaft	asymmetrical	asymmetrical	symmetrical
	Extension of the external tricipital groove visible in the palmar view	none	none	none
	Shape of the additional process on the ectepicondylar prominence	rounded, minute	rounded, minute	pointed, large
	Shape of the attachment of the pronator brevis	"D" shaped	"D" shaped	"D" shaped
	Depth of the attachment of the pronator brevis	deep	deep	shallow

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APPENDIX TABLE 8. Extended.

UF 27855, *Riparia riparia*	UF 27893, *Hirundo rustica*	UF 27863, *Stelgidopteryx ruficollis*	ROM 69716–69742, Fossil: *Petrochelidon rufocollaris*	LSUMZ 100541, *Petrochelidon rufocollaris*	UF 27803, *Petrochelidon pyrrhonota*
long	long	intermediate	short	short	short
intermediate, intermediate	rounded, intermediate	rounded, narrow	rounded, wide	rounded, wide	rounded, wide
intermediate	shallow	deep	shallow	shallow	shallow
symmetrical	asymmetrical	symmetrical	asymmetrical	asymmetrical	asymmetrical
none	none	none	none	none	none
rounded, minute	pointed, minute	absent	pointed, minute	pointed, minute	rounded, minute
rounded	"D" shaped	absent	rounded	rounded	"D" shaped
intermediate	shallow	very shallow–absent	intermediate	intermediate	intermediate

APPENDIX TABLE 9. Osteological characters used to identify *Myiodynastes bairdii* fossils using flycatcher species of similar size for comparison.

Element	Character	ROM 69706–69707, Fossil: *Myiodynastes bairdii*	UF 49306, *Myiodynastes bairdii*	UF 13678, *Pitangus sulphuratus*	UF 33887, *Myiarchus tyrannulus*
Humerus	Length of the ectepicondylar prominence	short	short	short	intermediate
	Shape of the curvature of the ectepicondylar prominence away from the shaft	narrow	narrow	wide	wide
	Depth of the curvature of the ectepicondylar prominence	shallow	shallow	very shallow	intermediate
	Symmetry of the curvature of the ectepicondylar prominence away from the shaft	symmetrical	symmetrical	asymmetrical	asymmetrical
	Extension of the external tricipital groove visible in the palmar view	absent	absent	absent	absent
	Shape of the additional process on ectepicondylar prominence	very shallow, rounded	very shallow, rounded	very shallow, rounded	nearly absent
	Shape of the attachment of the pronator brevis	round	round	round	round
	Depth of the attachment of the pronator brevis	very shallow	very shallow	very shallow	shallow

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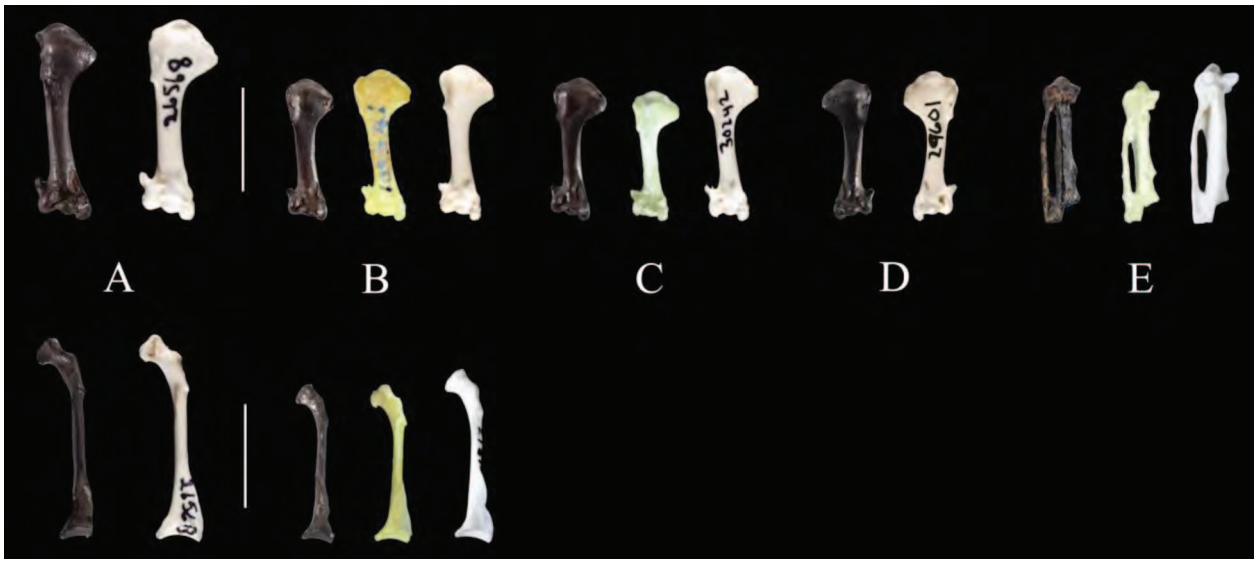
APPENDIX TABLE 10. Coracoid measurements of *Myiozetetes similis* subspecies and related flycatchers of comparable size as the *Myiozetetes* cf. *similis* fossil from Talara.

Taxa (UF)	Sex (M = Male, F = Female, U = Unknown)	Coracoid length (mm)
Fossil ROM 69705	U	18.75
Myiozetetes cayanensis cayanensis		
UF 27586	M	17.95
UF 27585	F	17.12
Myiozetetes similis texensis		
UF 13686	M	N/A
UF 27590	F	18.99
UF 27589	F	18.40
UF 27595	U	19.14
Myiozetetes similis columbianus		
UF 38618	M	18.11
UF 27593	M	18.88
UF 46254	M	19.21
UF 27592	M?	18.51
UF 27591	F	17.56
UF 27594	F	17.22
Myiozetetes granadensis granadensis		
UF 38617	M	18.58
UF 27587	M	18.74
UF 27588	F	18.12
Pitangus lictor		
UF 27681	U	16.83
Tyrannus savana		
UF 38997	M	18.91
Myiarchus semirufus		
UF 49296	F	15.76
Myiarchus tuberculifer atriceps		
UF 43494	M	17.78
Myiarchus phaeocephalus interior		
UF 49137	F	17.73
UF 49195	F	18.54
UF 49165	M	17.42
Myiarchus tyrannulus tyrannulus		
UF 49258	M	19.02
UF 49140	F	18.55

APPENDIX TABLE 11. Osteological characters used to identify *Thamnophilus bernardi* fossils.

Element	Character	ROM 69702–69704, Fossil	UF 49366, *Thamnophilus bernardi*
Humerus	Length of the ectepicondylar prominence	very short	very short
	Shape of the curvature of the ectepicondylar prominence away from the shaft	rounded	rounded
	Depth of the curvature of the ectepicondylar prominence	N/A	shallow
	Symmetry of the curvature of the ectepicondylar prominence away from the shaft	N/A	asymmetrical
	Extension of the external tricipital groove visible in the palmar view	slight	slight
	Shape of the additional process on the ectepicondylar prominence	rounded, minute	rounded, minute
	Shape of the attachment of the pronator brevis	rounded	rounded
	Depth of the attachment of the pronator brevis	shallow	shallow

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APPENDIX FIGURE 10. Postcranial elements of martins and swallows. (**A**) Humeri (top) and coracoids (bottom) of *Progne* species, with Talara fossil (*Progne* sp. fossil; humerus: ROM 69712; coracoid: ROM 69708) on left, and modern *Progne tapera tapera* (UF 27837; old catalogue number 26568, Suriname) on right. (**B**) Humeri (top) and coracoids (bottom) of *Petrochelidon* species, with Talara fossil (*Petrochelidon rufocollaris*; humerus: ROM 69716; coracoid: ROM 69743) on left, modern *Petrochelidon rufocollaris* (LSUMZ 100541) at center, and modern *Petrochelidon pyrrhonota pyrrhonota* (UF 27803; old PB catalogue number 21812, New Brunswick) on right. (**C**) Humeri of *Tachycineta* species with Talara fossil (*Tachycineta stolzmanni*; ROM 69715) on left, modern *Tachycineta stolzmanni* (LSUMZ 90118) at center, and modern *Tachycineta bicolor* (UF 27878; old PB catalogue number 30242, Florida) on right. (**D**) Humeri of *Hirundo rustica*, with Talara fossil (ROM 69763) on left, and modern specimen (UF 27893; old PB catalogue number 29601, Indiana) on right. (**E**) Carpometacarpi of *Petrochelidon* species, with Talara fossil *P. rufocollaris* (ROM 69755) on left, modern *P. rufocollaris* (LSUMZ 100541) at center, and modern *P. pyrrhonota pyrrhonota* (UF 27803; old PB number 21812, New Brunswick) on right. PB = collection of Pierce Brodkorb; now in UF collection. Scale bars = 10 mm.

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