The Pleistocene Burrowing Owl (*Athene cunicularia*) from The Bahamas

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Photo: Janet Franklin

Birds Caribbean

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Ajay M. Patel[1,2] and David W. Steadman*[1,3]

Abstract Modern populations of the Burrowing Owl (*Athene cunicularia*) occur locally from the western half of North America through Central America and into South America, as well as in Florida and on some Caribbean and Mexican islands. By comparing skeletal measurements, we assessed the morphological differences between late Pleistocene fossils of Burrowing Owls from Abaco, The Bahamas, where the species either no longer exists or is rare, and modern specimens from western North America, western South America, and Florida. The fossils from Abaco are significantly smaller in both wing and leg elements compared to their extant continental counterparts, especially those from western North America and South America. The relatively short distal leg elements of the insular Burrowing Owls may be associated with reduced predation pressure and the highly irregular substrate in much of the Bahamas, consisting primarily of weathered limestone bedrock rather than soft soils. Compared to continental populations, the Bahamian fossil specimens also have a relatively shorter distal wing (carpometacarpus) compared to the femur, which is an indicator of body size. In this, they conform to a general trend among insular birds capable of flight, which may be related to a reduced need for dispersal, migration, or rapid escape from predators.

Keywords Abaco, *Athene cunicularia*, geographic variation, insular adaptations, osteology, paleontology, The Bahamas

Resumen *Athene cunicularia* del Pleistoceno de las Bahamas • Las poblaciones modernas de *Athene cunicularia* se distribuyen localmente desde la mitad occidental de Norteamérica a través de América Central y América del Sur; así como, en Florida y algunas islas del Caribe y México. Mediante la comparación de las medidas esqueléticas, estimamos las diferencias morfológicas entre fósiles de esta especie del Pleistoceno tardío de Ábaco, Bahamas, donde la especie ya no existe o es rara, y especímenes modernos de las regiones occidentales de Norteamérica y Suramérica, además de Florida. Los fósiles de Ábaco son significativamente más pequeños, tanto en elementos del ala como de la extremidad inferior, comparados con sus contrapartes continentales, especialmente los del oeste de Norteamérica y Suramérica. Los elementos distales relativamente cortos de las extremidades inferiores de *Athene cunicularia* pueden estar asociados con una presión de depredación reducida y el sustrato altamente irregular de gran parte de las Bahamas, que consiste primariamente en un lecho de roca caliza erosionada en lugar de suelos blandos. Comparados con las poblaciones continentales, los especímenes fósiles de Bahamas también tienen un ala distal (carpometacarpo) relativamente más corta en comparación con el fémur, lo que es un indicador del tamaño corporal. En esto, se ajustan a una tendencia general entre las aves insulares capaces de volar, lo cual puede estar relacionado con una menor necesidad de dispersión, migración o un escape rápido de los depredadores.

Palabras clave Ábaco, adaptaciones insulares, *Athene cunicularia,* Bahamas, osteología, palentología, variación geográfica

Résumé Chevêche des terriers du Pléistocène (*Athene cunicularia*) des Bahamas • Les populations modernes de Chevêche des terriers (*Athene cunicularia*) sont présentes localement de la moitié ouest de l'Amérique du Nord, à l'Amérique centrale et jusqu'en Amérique du Sud, ainsi qu'en Floride et sur certaines îles de la Caraïbe et du Mexique. En comparant des mesures du squelette, nous avons évalué les différences morphologiques entre les fossiles de la fin du Pléistocène de Chevêche des terriers d'Abaco, aux Bahamas, où l'espèce n'existe plus ou est devenue rare, et les spécimens modernes de l'ouest de l'Amérique du Nord, de l'ouest de l'Amérique du Sud et de Floride. Les éléments des ailes et des pattes des fossiles d'Abaco sont significativement plus petits que ceux des espèces continentales actuelles, en particulier ceux de l'ouest de l'Amérique du Nord et de l'Amérique du Sud. Les éléments distaux relativement courts des pattes des Chevêches des terriers insulaires peuvent être associés à une pression de prédation réduite et au substrat très irrégulier dans une grande partie des Bahamas, constitué principalement de roches calcaires altérées plutôt que de sols meubles. Par rapport aux populations continentales, les spécimens fossiles des Bahamas présentent également une aile distale (carpométacarpe) relativement plus courte que le fémur, ce qui est un indicateur de la taille du corps. En cela, ils se conforment à une tendance générale parmi les oiseaux insulaires capables de voler qui peut être liée à un besoin réduit de dispersion, de migration ou de fuite rapide face aux prédateurs.

Mots clés Abaco, adaptations insulaires, *Athene cunicularia*, Bahamas, ostéologie, paléontologie, variation géographique

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In studying morphological evolution across a broad variety of insular birds, Wright and Steadman (2012) found that compared to conspecific populations on continents, many island populations have weak flight musculature relative to body mass. This weaker flight is often also associated with longer legs (Wright *et al.* 2017)—as seen, for example, in an extirpated population of the Eastern Bluebird (*Sialia sialis*) which occurred in the Bahamas during the Pleistocene (Steadman and Franklin 2017). These trends may be related to reduced predation pressure and other ecological shifts in island settings. On the other hand, a Pleistocene population of the Eastern Meadowlark (*Sturnella magna*) in the Bahamas had short distal leg elements relative to continental conspecifics, perhaps related to a reduced need for high running speed in a rugged karst terrain that lacked predatory mammals (Oswald *et al.* 2019). Relatively short distal leg elements also occurred in truly flightless Bahamian species, such as the rails *Rallus cyanocavi* and *R. gracilipes* (Steadman *et al.* 2013, Takano and Steadman 2018).

The purpose of this study is to compare and evaluate the morphology of another Bahamian species found abundantly in the fossil record: the Burrowing Owl (*Athene cunicularia*). Numerous complete and nearly complete fossils of this species have been retrieved from a blue hole, a large marine sinkhole, called Sawmill Sink on the island of Great Abaco, The Bahamas. These fossils are from the late Pleistocene (25,000–10,000 years ago) "Owl Roost" deposits at Sawmill Sink, where they were preserved after having been eaten and regurgitated as bony pellets by the larger Barn Owl, *Tyto alba* (Steadman *et al.* 2007, 2015a).

Burrowing Owls are a ground-dwelling species with a scattered distribution in the Bahamas today. As summarized by White (1998) and corroborated by more recent observations (Sullivan *et al.* 2009), Burrowing Owls may be common on Cat Island and Great Inagua, but are found only infrequently on other Bahamian islands (Table 1). Indeed, Currie *et al.* (2019) classify the Burrowing Owl in the Bahamas as "uncommon to rare, with a declining population."

Elsewhere in the West Indies, the modern range of the Burrowing Owl is less extensive than it once was. Fossils have been found on several islands where the species no longer occurs, including Jamaica (Olson and Steadman 1977), Cayman Islands (Morgan 1994), Mona (Olson and Hilgartner 1982), Puerto Rico (Pregill and Olson 1981), St. Eustatius, Barbuda, and Antigua (Pregill *et al.* 1994). Five West Indian subspecies of *Athene cunicularia* are recognized as follows (from Clark 1997, Wiley 1998, Gallardo and Thorstrom 2019): *A. c. floridana* (Florida, The Bahamas, western Cuba), *A. c. guantanamensis* (eastern Cuba), *A. c. troglodytes* (Hispaniola), *A. c. amaura* (St. Kitts, Nevis, Antigua; extinct), and *A. c. guadeloupensis* (Guadeloupe, Marie-Galante; extinct).

Methods

Comparative Osteology

The Sawmill Sink fossils are catalogued in the Vertebrate Paleontology Collection at the Florida Museum of Natural History, University of Florida (UF), on long-term arrangement with the National Museum of The Bahamas. We identified these fossils as Burrowing Owls through direct comparison with modern skeletons of Burrowing Owls and numerous other species of

small New World owls at UF. Fossils of Burrowing Owls also occur elsewhere in the Bahamian Archipelago (The Bahamas, and The Turks and Caicos Islands; Table 1). Because most non-Abaco fossils of Burrowing Owls are fragmentary, and thus cannot be used for measurement-based comparison, they are not included in our analyses. We did not analyze humerus length statistically because we could only collect this measurement from three fossils. We supplemented the modern UF specimens with others from the Louisiana State University Museum of Natural Science and the Smithsonian National Museum of Natural History (USNM). Unfortunately, the only three modern skeletal specimens available from any West Indian Burrowing Owl population are unsexed, incomplete specimens from San Salvador, The Bahamas (USNM 555532) and Dominican Republic (USNM 555768, 555769). Our direct comparisons of the Bahamian fossils were with modern specimens from Florida (*Athene cunicularia floridana*), western North America (Kansas, Texas, New Mexico, California, and Idaho; *A. c. hypugaea*), and western South America (Peru and Bolivia; *A. c. juninensis*), which are the three geographic regions from which we could accumulate substantial numbers of specimens.

Table 1. Status of the Burrowing Owl (*Athene cunicularia*) in the Bahamian Archipelago. Based in part on Clark (1997). Modern Status numbers from White (1998). eBird records (Sullivan *et al.* 2009) accessed 8 November 2019. Fossil information from Olson and Hilgartner (1982), Olson *et al.* (1990), Steadman *et al.* (2015a, 2007), Oswald and Steadman (2018), and herein. Islands not listed in this table lack evidence for the past or present occurrence of the Burrowing Owl. Abaco includes Elbow Cay; Andros includes South Joulters Cay; Cat includes Little San Salvador.

Island	Modern Status	Most Recent eBird Report	Fossils
New Providence	4	2011	X
Grand Bahama	4	2008	---
Abaco	4	2016	X
Bimini	4	2019	---
Andros	2	2019	X
Eleuthera	3	2009	X
Exumas	2	---	X
Cat	1	2019	X
San Salvador	3	1988	X
Long	4	---	X
Crooked-Acklins	4	---	---
Inagua	1	2019	---
Cay Sal	6	---	---
Middle Caicos	---	---	X

Modern Status categories (paraphrased from White 1998). 1, Easily found; may be found during a short visit in the proper season. 2, Readily found; present in good numbers and can be found with little effort. 3, Difficult to see; requires luck and a special effort. 4, Extremely difficult to find; no dependable location. 5, Very unlikely to be found; on the verge of extirpation. 6, Cannot be found; either extinct or extirpated. X, present; ---, no record.

Osteological nomenclature follows that of Baumel and Witmer (1993), supplemented as needed by terms in Howard (1929). The osteological characters provided in Olson and Hilgartner (1982) were useful in confirming the identity of the Sawmill Sink owl fossils as Burrowing Owls. To differentiate the fossils from any species of *Megascops* (screech-owls) or *Glaucidium* (pygmy-owls), we used the following diagnostic characters: on the coracoid, the glenoid facet (facies articularis humeralis) extends farther laterally; on the humerus, the epicondylar area (epicondylaris ventralis) is more rounded; on the carpometacarpus, the pisiform process (processus pisiformis) lies along long axis of metacarpal II (os metacarpus majus) rather than being located more internally (cranially); on the femur, the trochanteric ridge (crista trochanteris) is more prominent; on the tibiotarsus, the internal and external condyles (condylus medialis and condylus lateralis) are more slender and nearly parallel to each other and to the long axis of the shaft (corpus tibiotarsi); and the tarsometatarsus (also agreeing with some characters from Lo Coco *et al.* 2019) is more slender overall, with the proximal half of the anterior (dorsal) shaft (corpus tarsometatarsi) much more concave, and the distal trochlea IV relatively small and laterally oriented.

Data Analysis

We took measurements with a Pittsburgh Model 47256 digital caliper (Harbor Freight Tools, Calabasas, CA) accurate to 0.01 mm. We performed simple linear regressions in R (R Core Team 2017) to visualize morphological trends in the four populations of interest. As we cannot say whether any set of the Abaco fossils represents a single individual, we calculated the full range of measurements for the Bahamian fossils and incorporated them into our regression analyses as rectangles of potential values. Specifically, we compared the relationship between femur length and both the coracoid and carpometacarpus lengths. This allowed us to infer the possible morphological adaptions of insular Burrowing Owls. We used two-tailed t-tests assuming unequal variance as the primary method to analyze the data units (individual skeletal measurements). All assumptions for the Welch's t-test were satisfied. The normality of data sets with $n < 30$ was tested through the base Shapiro-Wilk's test function in R. Data sets with $n > 30$ do not require tests for normality, as supported by the Central Limit Theorem (Kwak and Kim 2017). The data were assumed to have unequal variance because the samples were innately unpaired, and the sample sizes differed. The variance (σ^2) was still calculated, and then compared between

Table 2. Skeletal measurements (in mm) of Burrowing Owls, with Mean, Range, and Sample Size (*n*).

Skeletal Element	Bahamian Fossils			Florida			Western North America			Western South America		
	Mean	Range	*n*	Mean	Range	*n*	Mean	Range	*n*	Mean	Range	*n*
Coracoid												
length	24.35	22.70–25.91	13	26.16	24.05–28.40	26	26.80	25.52–27.97	17	26.10	23.91–27.40	12
Humerus												
length	48.90	47.64–49.89	3	52.67	49.57–56.86	25	54.73	52.85–57.54	16	53.79	48.02–57.37	12
midshaft width	3.06	2.61–3.36	25	3.47	3.18–3.94	25	3.48	3.24–3.85	16	3.38	3.13–3.70	12
depth	2.90	2.63–3.82	23	3.05	2.78–3.44	25	3.15	2.90–3.44	16	3.19	2.97–3.56	12
distal width	8.13	7.58–8.39	9	8.54	7.83–9.34	25	8.99	8.66–9.38	16	8.99	8.24–9.59	12
Carpometacarpus												
length	27.32	26.58–28.53	6	30.86	28.99–33.14	26	32.34	30.51–34.66	14	30.26	26.55–32.97	12
proximal width	5.90	5.58–6.08	5	6.44	5.93–6.83	26	6.79	6.36–7.25	15	6.71	6.42–7.14	12
Femur												
length	35.84	32.89–37.64	23	36.85	35.67–37.94	20	38.41	37.30–40.10	17	37.96	34.55–40.31	11
midshaft width	2.86	2.53–3.30	82	2.86	2.52–3.43	20	2.98	2.74–3.26	17	2.97	2.71–3.26	12
distal width	6.47	5.62–7.07	27	7.06	6.49–7.51	20	7.39	6.96–7.78	17	7.20	6.64–7.57	11
Tibiotarsus												
length[a]	57.53	55.13–59.89	16	65.64	62.31–68.84	19	65.21	62.51–68.70	15	62.82	58.29–67.00	11
midshaft width	2.77	2.51–3.47	59	2.89	2.55–3.30	20	2.95	2.56–3.53	16	3.07	2.73–3.44	12
distal width	6.13	5.15–6.82	20	6.49	6.05–6.92	19	6.71	6.36–7.27	16	6.97	6.74–7.12	12
Tarsometatarsus												
length	40.36	38.02–42.68	7	45.13	41.81–48.44	20	46.45	42.77–48.95	15	44.65	40.34–47.81	12
proximal width	6.18	5.52–7.05	21	7.08	6.60–7.60	20	7.02	6.60–7.50	16	7.19	6.57–7.77	12
least width of shaft	2.52	2.04–3.07	51	2.50	2.27–2.97	20	2.56	2.24–3.00	16	2.69	2.35–3.08	12
distal width	6.64	6.21–7.14	40	6.96	6.57–7.52	20	7.13	6.82–7.79	15	7.18	6.59–8.02	12

[a] without cnemial crest.

the data sets to confirm its inequality. During our preliminary analysis, we found no significant differences in size between males and females ($p > 0.05$) within any of the three groups of modern specimens, so each of the four geographic samples includes males, females, and unsexed individuals. Clark (1997) also found no sexual dimorphism in external measurements of Burrowing Owls. The fossils from Abaco are unsexed.

Comparing measurements across the populations allows us to infer the possible morphological adaptations of insular Burrowing Owls. The null hypothesis is that the skeletal measurements of the fossils and those of extant populations are not significantly different, while the alternative hypothesis is that the skeletal measurements of the fossils and those of extant populations are significantly different. The large number of t-tests we compared ($n = 48$) resulted in a family-wise error rate of 91.5% (Cao and Zhang 2014), indicating a very high likelihood of at least one Type I error occurring in the pool of data. We counteracted this phenomenon by applying the Holm-Bonferroni method to yield adjusted α-values (Holm 1979). We performed post-hoc data corrections in Microsoft Excel.

Results

Our measurements (Table 2) and analyses (Table 3) focused on major skeletal elements of the pectoral girdle (coracoid), wing (humerus, carpometacarpus; Figs. 1, 2), and leg (femur, tibiotarsus, tarsometatarsus; Figs. 2, 3). The pectoral girdle and wing elements of the Abaco fossils were significantly smaller than the western North America and western South America groups in all six skeletal measurements analyzed (Table 3). Compared with the Florida population, the Abaco fossils were significantly smaller in five of the six measurements.

Measurements of leg elements also differed overall between the Abaco fossil population and the continental populations. These differences, however, were more marked between the Abaco fossils and the western North America and western South America populations, with the Abaco fossils being significantly smaller in 9 of 10 measurements, and significantly smaller than the Florida population in 6 of the 10 measurements (Table 3). Thus, the apparent trend toward insular dwarfism in Burrowing Owls is not expressed uniformly across all skeletal elements.

To learn more about where and the extent to which these differences are expressed, we compared coracoid length and carpometacarpus length to femur length, with measurements of the femur being reasonable proxies for body mass (Livezey 2003). Comparing the coracoid with the femur, the rectangle of potential values for the fossils overlaps with 5 Florida specimens,

Table 3. T-test *p*-values and Holm–Bonferroni adjusted α levels, comparing skeletal measurements of the Bahamian fossils versus those of three modern populations. Statistically significant comparisons (*p*-value < adjusted α) are in bold.

Skeletal Element	vs. Florida		vs. Western North America		vs. Western South America	
	p-values	α levels	*p*-values	α levels	*p*-values	α levels
Coracoid						
length	**2.97×10^{-6}**	**0.001471**	**1.55×10^{-8}**	**0.001250**	**0.000291**	**0.002381**
Humerus						
midshaft width	**2.76×10^{-9}**	**0.001190**	**7.99×10^{-10}**	**0.001136**	**8.65×10^{-5}**	**0.002000**
midshaft depth	0.019810	0.007143	**0.000232**	**0.002273**	**0.000292**	**0.002500**
distal width	**0.001247**	**0.003125**	**1.67×10^{-7}**	**0.001389**	**1.16×10^{-5}**	**0.001667**
Carpometacarpus						
length	**3.88×10^{-6}**	**0.001515**	**4.16×10^{-8}**	**0.001282**	**0.000307**	**0.002632**
proximal width	**0.001687**	**0.003571**	**3.10×10^{-5}**	**0.001724**	**4.83×10^{-5}**	**0.001786**
Femur						
length	**0.000901**	**0.002941**	**1.25×10^{-10}**	**0.001087**	**0.001361**	**0.003333**
midshaft width	0.978476	0.001000	**0.003561**	**0.004545**	0.058586	0.01
distal width	0.210405	0.012500	**1.01×10^{-11}**	**0.001064**	**1.94×10^{-6}**	**0.001429**
Tibiotarsus						
length[a]	**8.42×10^{-16}**	**0.001020**	**4.02×10^{-14}**	**0.001042**	**7.99×10^{-5}**	**0.001923**
midshaft width	0.012413	0.005556	0.010508	0.005	**0.000232**	**0.002174**
distal width	**0.001871**	**0.004167**	**7.83×10^{-6}**	**0.001563**	**7.47×10^{-9}**	**0.001220**
Tarsometatarsus						
Length	**0.000117**	**0.002083**	**9.24×10^{-6}**	**0.001613**	**0.000805**	**0.002778**
Proximal width	**5.04×10^{-10}**	**0.001111**	**2.30×10^{-9}**	**0.001163**	**4.88×10^{-8}**	**0.001316**
Least width of shaft	0.710170	0.025000	0.472433	0.016667	0.026157	0.008333
Distal width	**7.60×10^{-5}**	**0.001852**	**1.38×10^{-7}**	**0.001351**	**0.001840**	**0.003846**

[a] without cnemial crest.

Fig. 1. The coracoid (left, in ventral aspect) and humerus (right, in ventral aspect) of *Athene cunicularia*. A, E: UF 471248, UF 471250, fossils, Sawmill Sink, Abaco. B, F: UF 26459 (PB 23917), *A. c. floridana* ♂, Florida. C, G: UF 48253, *A. c. hypugaea* ♂, New Mexico. D, H: UF 26462 (PB 35356), *A. c. juninensis* ♂, Peru. Scale bar = 10 mm.
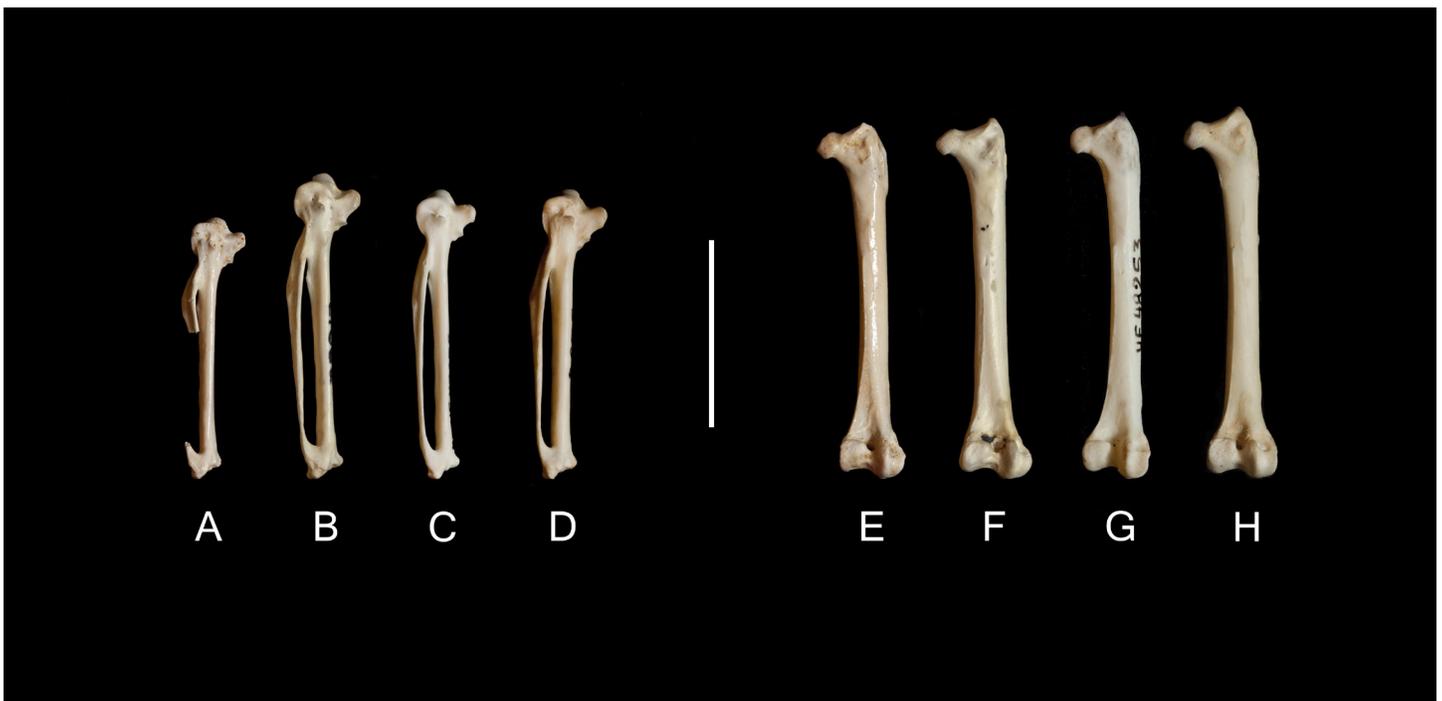
Fig. 2. The carpometacarpus (left, in ventral aspect) and femur (right, in ventral aspect) of *Athene cunicularia*. A, E: UF 471251, UF 471249, fossils, Sawmill Sink, Abaco. B, F: UF 26459 (PB 23917), *A. c. floridana* ♂, Florida. C, G: UF 48253, *A. c. hypugaea* ♂, New Mexico. D, H: UF 26462 (PB 35356), *A. c. juninensis* ♂, Peru. Scale bar = 10 mm.

Fig. 3. The tibiotarsus (left, in dorsal aspect) and tarsometatarsus (right, in dorsal aspect) of *Athene cunicularia*. A, E: UF 471252, UF 471253, fossils, Sawmill Sink, Abaco. B, F: UF 26459 (PB 23917), *A. c. floridana* ♂, Florida. C, G: UF 48253, *A. c. hypugaea* ♂, New Mexico. D, H: UF 26462 (PB 35356), *A. c. juninensis* ♂, Peru. Image reversed for UF 48253. Scale bar = 10 mm.
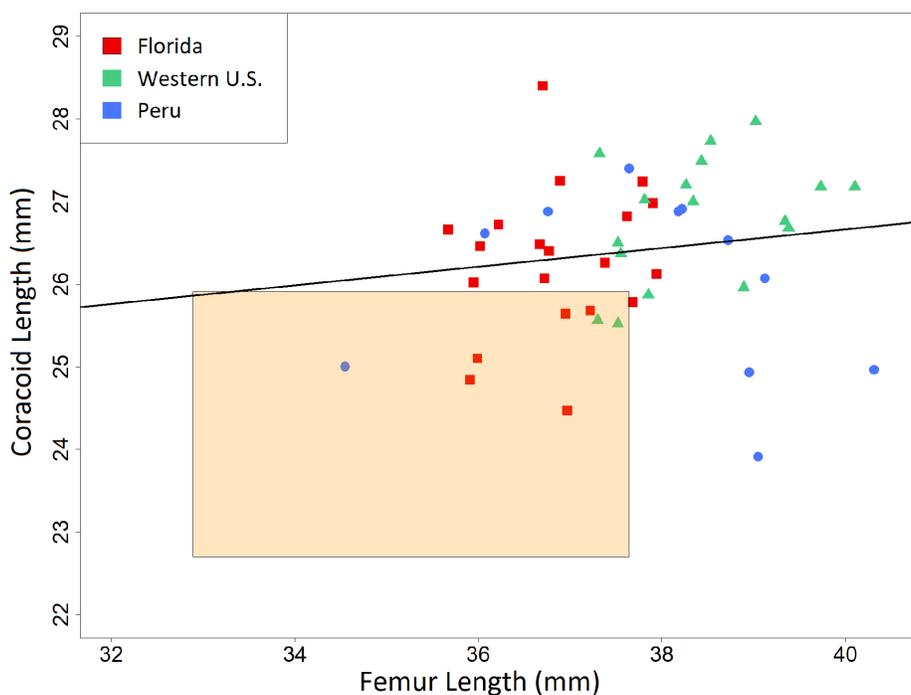
Fig. 4. Regression of length of coracoid vs. length of femur in four populations of Burrowing Owl. The tan rectangle encloses the full range of measured values for both coracoid length and femur length of the Bahamian fossils, which are not plotted as single points because we cannot say whether any one of those sets of measurements represents a single individual. For the line of best fit for the three modern populations, $r^2 = 0.02212$.
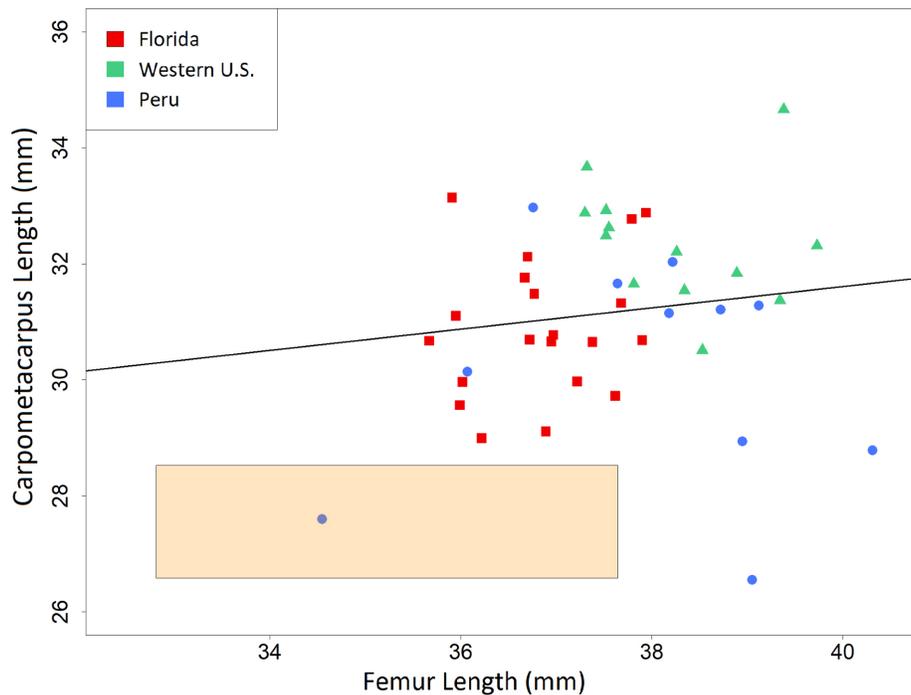
Fig. 5. Regression of length of carpometacarpus vs. length of femur in four populations of Burrowing Owl. The tan rectangle encloses the full range of measured values for both coracoid length and femur length of the Bahamian fossils, which are not plotted as single points because we cannot say whether any one of those sets of measurements represents a single individual. For the line of best fit for the three modern populations, $r^2 = 0.01921$.

2 western North America specimens, and 1 from Peru, with 39 modern specimens outside of the rectangle (Fig. 4; $r^2 = 0.02212$). Comparing femur length to carpometacarpus length, the differences are much more striking. The rectangle of potential values for the fossils overlaps with only a single modern specimen, from Peru (Fig. 5; $r^2 = 0.01921$). The proximal wing hinges on the coracoid, so Figures 4 and 5 indicate a greater shortening of the distal wing in the Abaco fossil population.

Discussion

Pleistocene fossils of Burrowing Owls have been reported from Florida, southwestern U.S., Venezuela, Ecuador, Peru, and Argentina, so the species has been widespread for a considerable time (Campbell 1976, 1979, Lundelius *et al.* 1983, Tonni 1983, Emslie 1998, Steadman *et al.* 2015b, Lo Coco *et al.* 2019). Our data from Abaco suggest that the Pleistocene Bahamian population of Burrowing Owl may have originated in Florida, which is not surprising given the geographic proximity of these two areas. However, given the paucity of modern West Indian skeletal specimens, and the scarcity of complete fossils of Burrowing Owls on Bahamian islands other than Abaco, we cannot be sure whether this is true for other populations in the West Indies. The relatively small amount of morphological differentiation between the Burrowing Owls in Florida and Abaco is compatible with their modern populations being classified as the same subspecies, *A. c. floridana*. The differences in skeletal measurements between these two populations, however, clearly supports some level of insular adaptation in the Abaco birds.

Our morphological results would be interesting to compare

with molecular genetic analyses, although, again, the paucity of modern West Indian specimens of Burrowing Owl (few skins, 3 partial skeletons, no tissues) precludes such analyses at this point. For example, Macías-Duarte *et al.* (2019) did not include any West Indian samples in their genetic analyses of Burrowing Owls. Nevertheless, we suspect that late Pleistocene gene flow occurred between Burrowing Owls in Florida and The Bahamas, especially given the large number of other species of birds shared between Florida and The Bahamas at that time (Steadman and Franklin 2015, 2017). We also note that the Florida population is genetically distinct from that of western North America (Macías-Duarte 2011, Macías-Duarte *et al.* 2019). The South American populations are likely genetically distinct as well, but remain unanalyzed. Finally, the low r^2 values (0.02212, 0.01921, respectively) in both regression models (Figs. 4, 5) might be explained by the outlying specimens, especially for Peru.

Based on its statistically significant smaller values for most pectoral girdle and wing measurements, as well as the relatively short distal wing (carpometacarpus), the Abaco population may have had a reduced need for sustained flight, whether for dispersal, seasonal migration, or evading predators, compared to any of the continental populations of Burrowing Owls. Previous research suggests that the rugged karst terrain in the Bahamas (Hearty *et al.* 1998, Mylroie and Mylroie 2013) and the absence of mammalian predators may be factors behind the short distal leg elements in some extirpated populations of ground-dwelling birds in the Bahamas, such as the meadowlark, *Sturnella magna*, and the rails, *Rallus cyanocavi* and *R. gracilipes* (Takano and Steadman 2018, Oswald *et al.* 2019). Among ground-dwell-

ing birds, elongated distal leg elements are associated with enhanced running speed (e.g., the Secretarybird *Sagittarius serpentarius*), which is not required in predator-free environments on remote islands, perhaps particularly on islands with irregular (e.g., pitted or pinnacled) ground surfaces. For example, flightless rails with relatively short distal leg elements have been described from other oceanic limestone islands, including Bermuda (Olson and Wingate 2000, 2001) and even in Polynesia (Steadman 1986, Kirchman and Steadman 2005). The flightless ibises (*Apteribis* spp.) from the Hawaiian Islands (Olson and James 1991) also seem to have had relatively short tarsometatarsi relative to other leg elements.

The fossil Burrowing Owl from Abaco conforms to this trend. It also conforms strongly to the insular trend of shortened distal wing elements, which occurs even in species that remain capable of flight, as seen in extinct West Indian woodcocks, snipes, and many other species (Takano and Steadman 2015, Steadman and Takano 2016, Wright *et al.* 2017).

Acknowledgments

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Title Page Illustration

Sawmill Sink, Abaco, The Bahamas, the site where the Burrowing Owl fossils were found. David Steadman is standing at the edge of the flooded sinkhole. Photo taken in January 2009 by Janet Franklin.

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