Historic Genetic Structuring and Paraphyly Within the Great-Tailed Grackle

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HISTORIC GENETIC STRUCTURING AND PARAPHYLY WITHIN THE GREAT-TAILED GRACKLE

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Abstract. The Great-tailed Grackle (*Quiscalus mexicanus*) and Boat-tailed Grackle (*Q. major*) are sister species that have expanded their ranges during historical times. This expansion has created an area of sympatry between these species in Texas and Louisiana, and between distinctive Great-tailed Grackle subspecies in the southwestern United States and northern Mexico. We investigated the evolutionary histories of both species using mitochondrial DNA sequence data and modern phylogenetic methods. Our results reveal genetic structure within Great-tailed, but not Boat-tailed Grackles. Great-tailed Grackles are separated into two clades, but range expansion in the north has led to secondary contact between them. Boat-tailed Grackles are monophyletic and are embedded within the Great-tailed Grackle assemblage, rendering the latter paraphyletic. These results reveal a complex phylogeographic pattern caused by recent range expansion and secondary contact of once allopatric units.

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Key words: grackle, mitochondrial DNA, paraphyly, phylogeography, Quiscalus*, range expansion.*

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Estructuramiento Genético Histórico y Parafilia de *Quiscalus mexicanus*

Resumen. *Quiscalus mexicanus* y *Q. major* son especies hermanas que han expandido sus ámbitos de distribución durante tiempos históricos. Estas expansiones han creado un área de simpatría entre las dos especies en Texas y Louisiana, y entre subespecies distintivas de *Q. mexicanus* en el suroeste de los Estados Unidos y el norte de México. Investigamos las historias evolutivas de ambas especies usando secuencias de ADN mitocondrial y por medio de métodos filogenéticos modernos. Nuestros resultados revelaron estructura genética dentro de *Q. mexicanus*, pero no dentro de *Q. major*. *Q. mexicanus* está separada en dos clados, pero la expansión de su rango en el norte ha permitido el contacto secundario entre éstos. *Q. major* forma un grupo monofilético que está embebido dentro del ensamble del *Q. mexicanus*, lo que hace que *Q. mexicanus* sea un grupo parafilético. Estos resultados revelan un patrón filogeográfico complejo causado por la expansión reciente de sus ámbitos de distribución y el contacto secundario de unidades que anteriormente estaban en alopatría.

The Great-tailed Grackle (*Quiscalus mexicanus*) and Boat-tailed Grackle (*Q. major*) are sister species (Bjørklund 1991, Johnson and Lanyon 1999) that, until the mid-20th century, were considered conspecific as *Cassidix mexicanus* (AOU 1957). Great-tailed Grackles range from coastal Peru to Venezuela in South America, and throughout Central America, Mexico, and much of the continental United States west of the Mississippi River (Johnson and Peer 2001). They breed in a wide variety of habitats including marshes, mangroves, pastures, agricultural land, and suburban to urban environments (Johnson and Peer 2001). In contrast, Boat-tailed Grackles are restricted to coastal habitats from eastern Texas to Connecticut, except for Florida and southern Georgia, where they occur inland (Post et al. 1996, McNair and Baker 2000). The range of the Great-tailed Grackle has undergone a considerable and rapid expansion in the United States in the last century (Wehtje 2003), creating a zone of sympatry in Texas and Louisiana with the Boat-tailed Grackle. A study of morphological and behavioral differences between the species in this zone of sympatry concluded that, while hybridization is possible, there is a lack of large-scale introgression between species due to behavioral isolating factors (Selander and Giller 1961). However, the notion of reproductive isolation between these grackles has been challenged (Phillips et al. 1964), and hybrids have since been documented in Louisiana (Pratt 1991).

A high degree of intraspecific morphological diversity in the widespread Great-tailed Grackle is reflected by its division into eight subspecies (Johnson and Peer 2001). The northern subspecies *nelsoni*, *monsoni*, and *prosopidicola* occur in the United States and northern Mexico, from west to east, respectively. The subspecies *graysoni* (Sinaloa), *obscurus* (Nayarit to Guerrero), and *loweryi* (Yucatán) have restricted ranges in coastal areas of Mexico. The nominate form, *mexicanus*, is widespread from central Mexico to Panama, and *peruvianus* is distributed in the coastal northwestern regions of South America. Differences among these subspecies consist primarily of variations in body size and female plumage color (WW, pers. obs.).

The more geographically restricted Boat-tailed Grackle is comprised of four subspecies (Post et al. 1996). The subspecies *torreyi* breeds from Connecticut to northern Florida, while *westoni* is distributed throughout the Florida peninsula. The subspecies *major* and *alabamensis* breed along the western and northern Gulf of Mexico coast, respectively. Boat-tailed Grackle subspecies designations are based upon differences in morphology and iris color (Stevenson 1978).

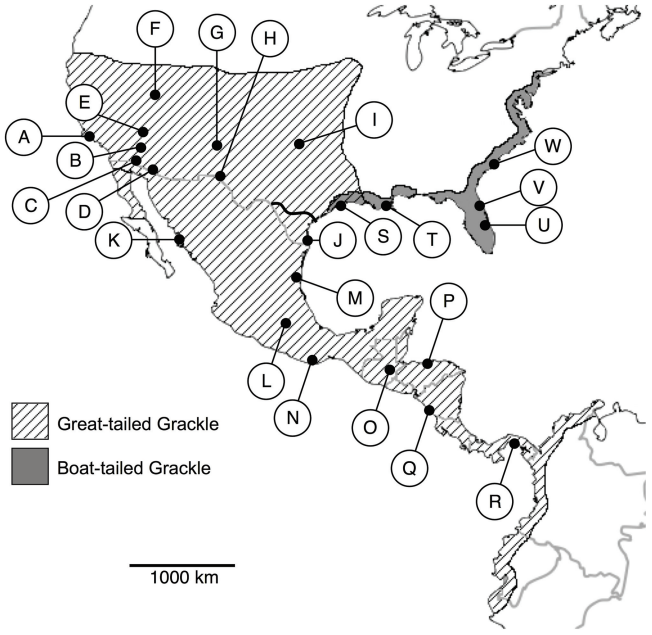

FIGURE 1. Approximate distributions and sampling localities for Great-tailed and Boat-tailed Grackles. All samples from the area of sympatry (locality S) are of Boat-tailed Grackles. The bold line in southern Texas represents the approximate range of the Great-tailed Grackle in the United States in 1880 (Wehtje 2003).

Modern molecular techniques offer a powerful tool to analyze the structuring of genetic diversity within and the relationships among the subspecies of the Great-tailed and Boat-tailed Grackle complex. A recent analysis of the mitochondrial DNA (mtDNA) cytochrome-*b* and NADH dehydrogenase subunit 2 (ND2) genes in blackbirds confirms that these species are sister species (Johnson and Lanyon 1999). However, because only one sample of each species was included in the study, it was impossible to test for monophyly or examine intraspecific genetic variation (Avise 2000, Funk and Omland 2003). Studies of widely distributed taxa in Mexico and Central America (Sullivan et al. 2000, Castoe et al. 2003, Eberhard and Bermingham 2004, Garcia-Moreno et al. 2004, Hasbun et al. 2005, Wuster et al. 2005, Mulcahy et al. 2006) and along the Atlantic coast of the United States (Avise 1996) have repeatedly recovered geographic patterns of genetic structure in a wide variety of vertebrates. Geographic features identified in these studies as having played an important role in the genetic structuring of populations include the Isthmus of Tehuantepec, the Sierras (Occidental and Oriental) of Mexico, and the Florida Peninsula. Because the distributions of Great-tailed and Boat-tailed Grackles collectively traverse these same barriers, similar patterns of genetic structuring might be expected. Here we analyze mtDNA sequence data from an expanded set of Great-tailed and Boat-tailed Grackle samples to investigate relationships between, and diversity within, these species.

METHODS

SAMPLING

Our sampling strategy included birds from throughout the geographic distributions of Great-tailed and Boat-tailed Grackles (Fig. 1), although additional sampling, particularly in Central

TABLE 1. Locality and voucher data for Great-tailed and Boat-tailed Grackle samples analyzed. Refer to Figure 1 for localities corresponding to letters.

Species	Locality	*N*	Collecting locality	Museum[a]	Prep number
Quiscalus mexicanus	A	4	USA: California, Ventura County, Oxnard-Ojai	LACM	WW173
				LACM	WW186
				LACM	WW196
				LACM	WW209
	B	4	USA: Arizona, La Paz County, Lake Havasu	LACM	WW188
				LACM	WW214
				AMNH	WW236
				AMNH	WW237
	C	4	USA: Arizona, La Paz County, Cibola National Wildlife Refuge	AMNH	WW242
				AMNH	WW245
				AMNH	WW247
				AMNH	WW248
	D	4	USA: Arizona, Santa Cruz County, Pena Blanca Lake	LACM	WW191
				LACM	WW192
				LACM	WW193
				LACM	WW194
	E	4	USA: Nevada, Clark County, University of Nevada Las Vegas	MBM	JMD977
				MBM	JMD979
				MBM	JMD1005
				MBM	JMD1006
	F	4	USA: Nevada, Elko County, Ruby Lake	LACM	KLW870
				LACM	KLW873
				LACM	WW207
				LACM	WW212
	G	4	USA: New Mexico, Valencia County, Belen	MSB	RWD24666
				MSB	WW249
				MSB	WW250
				MSB	WW252
	H	4	USA: Texas, El Paso County, El Paso	MBM	JMD1020
				MBM	JMD1021
				MBM	JMD1022
				MBM	JMD1023
	I	1	USA: Oklahoma, Canadian County, El Reno	MBM	JMD312
	J	4	USA: Texas, Cameron County, Brownsville	MSB	RWD21685
				MSB	RWD21686
				MSB	RWD21687
				MSB	RWD22906
	K	4	Mexico: Sonora, Huatabampo	MBM	JK03387
				MBM	JK03388
				MBM	JK03389
				MBM	JK03390
	L	2	Mexico: Distrito Federal, Mexico City	MBM	JMD496
				MBM	JMD497
	M	1	Mexico: Tamaulipas, Gomez-Farias	MBM	DHB5763
	N	1	Mexico: Oaxaca, Oaxaca	CNAV	PO26660
	O	4	Guatemala: Guatemala and Zacapa	WFVZ	RC2783
				WFVZ	RC2786
				WFVZ	RC2803
				WFVZ	RC2807
	P	3	Honduras: Copan and Atlantida	MBM	DHB3199
				MBM	DHB3429
				MBM	DHB3756
	Q	3	Nicaragua: Matagalpa and Managua	MBM	DAB980
				MBM	DAB994
				MBM	DAB1354

(*Continued on next page*)

TABLE 1. (continued)

Species	Locality	*N*	Collecting locality	Museum[a]	Prep number
	R	4	Panama: Panama, Felipillo	MBM	GMS937
				MBM	GMS938
				MBM	GMS945
				MBM	GMS946
Q. major	S	4	USA: Texas, Jefferson County, Big Hill Bayou	MBM	JMD349
				MBM	JMD352
				MBM	JMD361
				MBM	JMD365
	T	4	USA: Louisiana, Terrebonne Parish, Pointe-au-chien	MBM	JMD330
				MBM	JMD331
				MBM	JMD333
				MBM	JMD335
	U	4	USA: Florida, Osceola, Three Lakes	MBM	JMD354
				MBM	JMD356
				MBM	JMD357
				MBM	JMD358
	V	1	USA: Florida, St. Johns County, St. Augustine	MBM	JMD380
	W	1	USA: South Carolina, Charleston County, Charleston	MBM	JMD346

[a]AMNH = American Museum of Natural History, CNAV = Colección Nacional de Aves, Universidad Nacional Autónoma de México, LACM = Natural History Museum of Los Angeles County, MBM = Marjorie Barrick Museum of Natural History, MSB = Museum of Southwestern Biology, WFVZ = Western Foundation of Vertebrate Zoology.

America, would likely increase the resolution of the phylogeographic analyses. We analyzed 59 Great-tailed Grackle samples (from four of eight subspecies) from six countries, and 14 Boat-tailed Grackle samples (from three of four subspecies) from four U. S. states (Table 1). GenBank sequences from three additional *Quiscalus* species [the Common Grackle (*Q. quiscula*), Greater Antillian Grackle (*Q. niger*), Carib Grackle (*Q. lugubris*)] were included in the analysis, and two *Euphagus* species [the Rusty Blackbird (*E. carolinus*) and Brewer's Blackbird (*E. cyanocephalus*)] were used as outgroups (Johnson and Lanyon 1999). Sequences produced by this study have been deposited in GenBank (accession numbers EU414537–609).

LABORATORY PROTOCOLS

We extracted total genomic DNA from all samples using a DNeasy Tissue Kit (Qiagen, Inc., Valencia, California) following the manufacturer's protocol. We then amplified ND2 using polymerase chain reaction (PCR). ND2 was amplified with the flanking primers L5215 (Hackett 1996) and H6313 (Johnson and Sorenson 1998) or HTrpC (Pérez-Emán 2005), and in some cases, the internal primers L5758 and H5766 (Johnson and Sorenson 1998). Amplifications were conducted in 12.5 μl reactions under conditions described previously (Klicka et al. 2005). Products were purified using the enzyme mixture ExoSAP-IT (USB Corporation, Cleveland, Ohio) following the manufacturer's protocol. We prepared 20 μl sequencing reactions using a Big Dye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California) with 0.5 μl of Big Dye and 20–40 ng of purified PCR product. Sequencing reactions were purified using the CleanSEQ (Agencourt Bioscience Corporation, Beverly, Massachusetts) magnetic bead clean-up, and run on an ABI 3100-*Avant* automated sequencer (Appied Biosystems, Foster City, California). We used the program Sequencher (Gene Codes Corporation, Ann Arbor, Michigan) to unambiguously align complementary strands, detect gaps in the sequences, and translate the data into amino acid form.

PHYLOGENETIC ANALYSES

Phylogenetic hypotheses were constructed using both maximum parsimony and maximum likelihood approaches. We used PAUP* 4.0b10 (Swofford 2002) to conduct unweighted maximum parsimony analyses with 10 random stepwise additions. Maximum parsimony nodal support was evaluated with 100 heuristic bootstrap pseudoreplicates, each with 10 random stepwise additions. We used MrModeltest 2.2 (Nylander 2004) to determine the most appropriate model of molecular evolution. The Akaike Information Criterion option was chosen (Posada and Buckley 2004), and it identified the general time reversible with a proportion of invariable sites (GTR + I) model as the best fit for the data. We used PAUP* to construct a maximum likelihood phylogeny using the parameter settings determined by MrModeltest. Maximum likelihood nodal support was evaluated with 100 bootstrap replicates using the program PhyML (Guindon and Gascuel 2003). Nodes recovered in 70% or more of the replicates in both the maximum parsimony and likelihood bootstrap analyses were considered well supported.

We used Bayesian inference in the program MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) to provide another measure of relationships and clade reliability. Analyses were run with random starting trees and four (three heated and one cold, default temperature setting of 0.2) Markov chain Monte Carlo chains. Two runs were performed with 25 000 000 generations and sampling every 1000 generations. Plots of the posterior probabilities of clades as a function of generation number using AWTY (Wilgenbusch et al. 2004) revealed that stationarity was reached well before 1 000 000 generations, and we conservatively discarded the first 5 000 000 generations as burn-in. Convergence across runs was confirmed by similar results between runs, low standard deviations of split frequencies in MrBayes, and

a comparison plot of the posterior probabilities of both runs using AWTY. Therefore, we combined the results from both runs to form a posterior distribution of 40 000 topologies. A 50% majority consensus tree was constructed from this distribution of topologies, and nodes with posterior probabilities of 95% or greater were considered significantly supported.

We evaluated the monophyly of Great-tailed Grackles and Boat-tailed Grackles through topology testing and analysis of the Bayesian posterior distribution. Using the same maximum likelihood parameters as in the unconstrained analysis, we constructed a topology in PAUP* with both species constrained as monophyletic. Constrained versus unconstrained likelihood scores were compared using the Shimodaira-Hasegawa (1999) test and the approximately unbiased test (Shimodaira 2002) in CONSEL (Shimodaira and Hasegawa 2001). In addition, the posterior distribution of the Bayesian analysis (40 000 topologies) was examined for topologies in which the species were monophyletic.

RESULTS

The complete sequence dataset (1041 base pairs) yielded 176 variable and 95 parsimony informative sites. Analysis of the 59 Great-tailed Grackle samples yielded 17 unique haplotypes, and that of the 14 Boat-tailed Grackle samples produced five. Intraspecific diversity was high in the Great-tailed Grackle (uncorrected pairwise *p*-distance ranging from 0%–2.4%) compared to the Boat-tailed Grackle (uncorrected pairwise *p*-distance ranging from 0%–0.2%). Phylogenetic reconstructions using maximum parsimony, maximum likelihood, and Bayesian methods produced very similar topologies with differences only among short terminal branches; therefore, only the maximum likelihood topology is shown (Fig. 2). The three methodologies of evaluating nodal support were generally consistent across clades.

The Great-tailed Grackle was recovered as paraphyletic with respect to the Boat-tailed Grackle (Fig. 2). Species monophyly was rejected in the Shimodaira-Hasegawa ($P = 0.03$) and approximately unbiased ($P = 0.006$) tests, and was not recovered in any of the 40 000 topologies in the Bayesian posterior distribution. There is a well-supported Great-tailed Grackle clade that is distributed in Sonora, Mexico; coastal California; and the southwestern United States (Fig. 2, Clade A). This clade corresponds well with the distribution of the westernmost subspecies, *nelsoni*. The remaining Great-tailed Grackle sequences are embedded in a well-supported sister clade that also includes all Boat-tailed Grackle sequences (Fig. 2, Clade B). Genetic structuring is evident among the Great-tailed Grackles in this clade (Fig. 2, subclades C and D). Clade C is comprised of sequences of Great-tailed Grackle samples from Tamaulipas, Texas, Oklahoma, New Mexico, Arizona, and Nevada. This clade contains all sequences from samples collected in the geographic distribution of the subspecies *prosopidicola*, and also some from within the geographic range of *monsoni.* Clade D contains sequences from samples collected in Arizona, New Mexico, and Nevada and contains individuals from within the geographic distribution of the subspecies *monsoni* and *nelsoni*. Great-tailed Grackle sequences from central Mexico to Panama form two clades, with sequences from the same localities found in both clades. However, these clades are not strongly supported, and their precise relationship to other grackles in Clade B could not be resolved with these data. The Boat-tailed Grackles comprise a well-supported monophyletic group (Fig. 2, Clade E), but with comparatively less intraspecific genetic diversity than Great-tailed Grackles.

DISCUSSION

By producing sequence data from multiple individual Great-tailed and Boat-tailed Grackles over a wide geographic area, we provided a more comprehensive evaluation of the relationship between these two species than previous molecular studies have. Our results indicate that the Great-tailed Grackle, as presently recognized, is paraphyletic; some Great-tailed Grackle sequences were more closely related to those of the Boat-tailed Grackle than to those of some sampled conspecifics (Fig. 2, Clade B). The clade of Great-tailed Grackles that is sister to the Boat-tailed Grackle is not limited in distribution to an area near the zone of sympatry, as samples from it represent birds ranging from Panama to Arizona. The only samples collected from the zone of sympatry between the two species were from eastern Texas (Fig. 1, locality S). Here, samples were obtained from birds in a coastal marsh, which is a habitat type where Boat-tailed Grackles are common and Great-tailed Grackles occur less frequently. All of these individuals were consistent in morphology with Boat-tailed Grackles, and genetically, fell within the Boat-tailed Grackle clade. However, our limited sampling in the zone of sympatry and our analysis of matrilineally inherited mtDNA do not provide the resolution necessary to adequately investigate the possibility of current hybridization or introgression between these species.

Species-level paraphyly can be caused by a variety of mechanisms including interspecific hybridization, incomplete lineage sorting, imperfect taxonomy, and unrecognized paralogy (Funk and Omland 2003). In species with shallow genetic divergences, it is difficult to differentiate among these potential causes. The phylogeography of the Great-tailed Grackle complex is perhaps most consistent with a scenario of peripheral isolate speciation (Funk and Omland 2003), with the embedded Boat-tailed Grackle resulting from the budding of a historic population in the eastern periphery of the ancestral distribution of the complex. However, the single gene tree produced in this study could be consistent with multiple histories, and additional loci and analyses that account for the stochastic variance in genetic processes are needed to statistically differentiate among the potential causes of paraphyly (Knowles and Maddison 2002, Peters et al. 2007). An extended study of these species with increased taxonomic and genomic sampling and population genetic analyses is in progress (JD, unpubl data).

These results demonstrate that the Great-tailed Grackle complex contains deep mtDNA structure, but the precise geographic boundaries are difficult to define with these data. The genetic structuring of samples from central Mexico to Panama could not be confidently described. It is possible that adding representation from the four unsampled subspecies in Mexico (*graysoni*, *obscurus*, *loweryi*, and *peruviensis*) to our analysis would provide additional resolution. The Sierra Madre Occidental and Sierra Madre Oriental in Mexico have presumably served as a barrier to gene flow in the evolutionary history of this predominantly lowland species. The pre-1900 ranges of the subspecies *nelsoni* (Pacific coast), *monsoni* (interior), and *prosopidicola* (Gulf coast) in northern Mexico are consistent with allopatric divergence caused by these mountain ranges; however, our sparse sampling in Mexico and the use of one locus in analyses preclude coalescent analyses that are needed to test this hypothesis. Recent northward expansion into the United States (Wehtje 2003) has created overlap in the distributions of these subspecies, which has blurred the boundaries previously delineated by morphological distinctions (Wehtje 2004). Expansion and overlap of divergent populations is supported in this study, where multiple localities

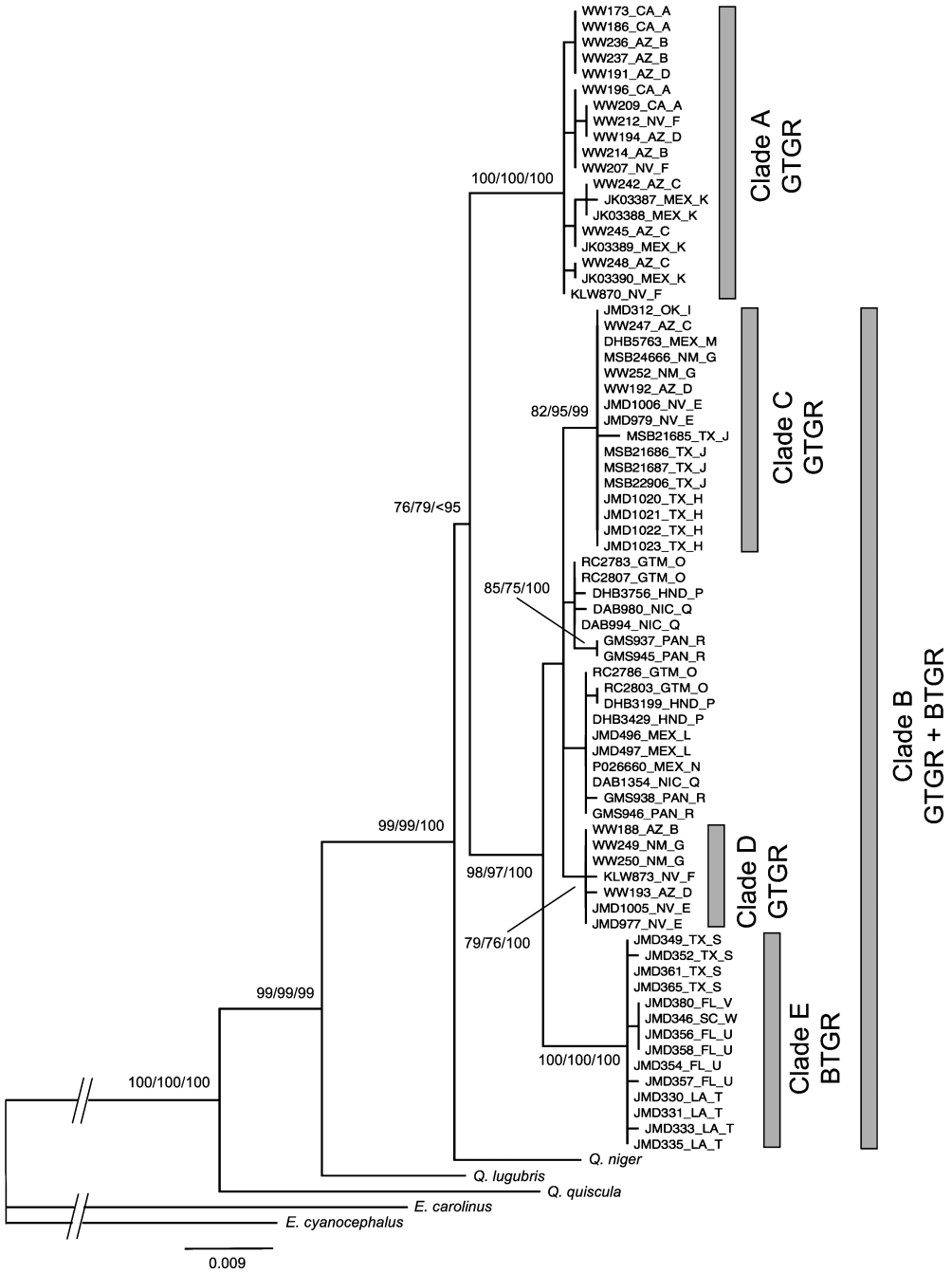

FIGURE 2. Maximum-likelihood topology of the relationships among Great-tailed (GTGR) and Boat-tailed (BTGR) Grackle samples. Terminal labels are prep numbers followed by a two-letter state (USA) or three-letter country (Central America) abbreviation and locality label (Fig. 1, Table 1). Numbers at nodes represent maximum parsimony and likelihood bootstrap, and Bayesian posterior probability values, respectively. All nodes without numbers were poorly supported (less than 70% bootstrap or 95% Bayesian posterior probability). Clades marked with shaded bars and letters are referred to in the text.

in the United States contained samples that were found in more than one well-supported clade.

Sampled sequences from the Boat-tailed Grackle show a comparatively shallow mtDNA history. There were shared haplotypes among sampled localities from the coasts of the Atlantic and Gulf of Mexico. This result is not surprising considering that Boat-tailed Grackles have less intraspecific morphological variation than Great-tailed Grackles. Polymorphisms of genetic loci controlling variable Boat-tailed Grackle phenotypic traits (e.g., iris color) are not reflected in the presumably neutral

mtDNA data presented here. Instead, these data illustrate a lack of genetic structure across the distribution of the species and suggest a recent coalescent history.

These results, in light of the recent range expansion of these species, pose an interesting taxonomic conundrum. Only 100 years ago, the Boat-tailed Grackle and multiple Great-tailed Grackle clades were likely in complete allopatry (Wehtje 2003) and formed geographically distinct and evolutionarily independent phylogenetic units in Central America and the United States. Recent and rapid range expansion (Wehtje 2003) has resulted in two zones of sympatry among these units. In the southwestern United States, divergent Great-tailed Grackle clades now have considerable geographic overlap and presumably interbred freely given that there is no evidence of isolating mechanisms. There is also overlap in the ranges of the Great-tailed and Boat-tailed Grackles along the western coast of the Gulf of Mexico. Although these units have a shallower mtDNA history, they are believed to be reproductively isolated due to behavioral mechanisms (Selander and Giller 1961). This scenario is similar to that of the Common (*Corvus corax*) and Chihuahuan (*C. cryptoleucus*) Ravens, where the monophyletic Chihuahuan Raven is embedded within the paraphyletic Common Raven (Omland et al. 2000). Similar to ravens, delimiting species boundaries in the Great-tailed Grackle complex depends on the species concept applied and interpretations of the data, and is further complicated by the low levels of morphological variation in the group. More behavioral and genetic data are needed from these zones of sympatry to gain a better understanding of possible introgression and taxon limits.

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A CLASSIFICATION-TREE ANALYSIS OF NESTING HABITAT IN AN ISLAND POPULATION OF NORTHERN HARRIERS

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Abstract. Nantucket Island, Massachusetts, hosts the largest population of breeding Northern Harriers (*Circus cyaneus*) in the northeastern United States. We analyzed 128 nest sites to determine landscape features influential to habitat selection. We performed a vegetation community use-availability study, and we used 70 GIS-derived landscape metrics to conduct a classification tree analysis. We used the classification tree results to quantify, predict, and map the preferred nesting habitat of harriers islandwide. The vegetation community use-availability study showed that harriers had a preference for herbaceous

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