The Island Syndrome in Coastal Wetland Ecosystems: Convergent Evolution of Large Bills in Mangrove Passerines

Authors: Luther, David, and Greenberg, Russell

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RAPID COMMUNICATIONS

THE ISLAND SYNDROME IN COASTAL WETLAND ECOSYSTEMS: CONVERGENT EVOLUTION OF LARGE BILLS IN MANGROVE PASSERINES

David Luther[1,2,3] and Russell Greenberg[2]

[1]*Biology Department, George Mason University, MS 3E1, Fairfax, Virginia 22030, USA; and*
[2]*Smithsonian Migratory Bird Center, Smithsonian Institute, National Zoo, Washington, D.C. 20008, USA*

Abstract.—Passerine birds on islands tend to have larger bills than their mainland relatives. The morphological shift may be related to reduced interspecific and increased intraspecific competition. Emberizid sparrows in North American salt marshes also show consistently greater bill size. We tested the hypothesis that passerines restricted to mangrove forests, another continental system with low species diversity and high population densities, also have larger bills than their closest nontidal relatives. We found a consistent pantropical pattern of longer and deeper bills in passerine birds restricted to mangroves. These results indicate that disproportionately longer bills in relation to body size in passerines restricted to coastal saline habitats, just like those found on islands, seems to be a general ecological rule. The similar pattern in bill morphology suggests that ecological and evolutionary processes thought to occur only in island systems might also occur in some continental systems. *Received 16 November 2010, accepted 31 January 2011.*

Key words: bill morphology, birds, dominance hypothesis, ecological convergence, mangrove, niche variation.

El Síndrome de Isla en Ecosistemas de Humedales Costeros: Evolución Convergente de Picos Grandes en Aves de Manglares

Resumen.—Las aves paserinas que viven en islas tienden a tener picos más grandes que sus parientes continentales. Los cambios morfológicos podrían estar relacionados con la reducción de la competencia intra e interespecífica. Los gorriones emberízidos que habitan marismas de Norteamérica también presentan picos de tamaños consistentemente mayores. Pusimos a prueba la hipótesis de que los paserinos restringidos a bosques de manglares, otro sistema continental con baja diversidad de especies y con altas densidades, también tienen picos más grandes que los de sus parientes más cercanos no asociados con sistemas intermareales. Encontramos un patrón pantropical consistente de picos más largos y profundos en aves paserinas restringidas a manglares. Estos resultados indican lo que parece ser una regla ecológica general: las aves paserinas restringidas a hábitats costeros salinos presentan picos desproporcionadamente más largos en relación con su tamaño corporal, tal como se ha encontrado en islas. El patrón similar en la morfología del pico sugiere que los procesos ecológicos y evolutivos que se pensaba que ocurrían sólo en sistemas insulares pueden ocurrir también en algunos sistemas continentales.

Islands have long been a natural laboratory for the study of ecological and evolutionary processes. Common features of vertebrate populations on islands have led to the development and refinement of "the island syndrome," which is characterized by low levels of interspecific competition and predation, high population densities, and ecological niche expansion.[1,2,3] Under these unique conditions, specific patterns of morphological divergence, such as larger or smaller body size compared with continental populations, have been associated with taxa that have successfully colonized islands.[4,5]

[3]E-mail: dluther@gmu.edu

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Among passerine birds, a trend toward increased bill size on islands has been well documented.[6,7] Larger bill size may be associated with a shift toward greater generalization in resource use.[8] Alternatively, larger bill size may confer behavioral dominance where resource use is mediated by behavioral competition in the social interactions associated with high population densities.[7] In both cases the hypotheses for the convergent morphological pattern of larger bill sizes on islands have been based on theories of ecological competition.

A persistent question in the fields of ecology and evolution is the degree to which island systems show processes that are unique and not comparable to continental systems. Greenberg and Olsen[9] proposed that the biotas of coastal marshes display many of the features characteristic of true islands, including low species diversity and high population densities, and that this has resulted in the consistent evolution of larger[10] and more dimorphic[9] bill sizes among different species and populations of emberizid sparrows (Passeriformes). Thus, salt marshes are continental ecosystems that seemingly have processes similar to those found on islands.

The question we address here is whether the patterns found in tidal-marsh sparrows can be found in other continental ecosystems that show both relatively high productivity and environmental constraints. Although physiognomically quite distinct from tidal marshes, mangrove forests share many of the same ecological features and replace tidal marshes along low-energy tropical shorelines.[11] As an ecotone between the marine and terrestrial realms, both tidal marshes and mangroves have vegetative strata that are similar to inland terrestrial ecosystems, an intertidal benthic component that is similar to the marine environment, moderate to high salinity levels, and low levels of floristic diversity.[11] Finally, predictable tidal inundation and less predictable storm-related flooding events can place severe constraints on terrestrial species in these habitats.[12,13]

Like tidal marshes, mangroves have lower avian species richness than adjacent terrestrial habitats.[13,14,15] On the other hand, the overall density of birds in mangrove and lowland humid rainforest seems to be relatively similar at least in Southeast Asia, although the majority of individuals in mangrove forests are from a few very abundant species.[14,15] Similarly, in northern Australian mangroves, five avian species accounted for 75% of all individuals detected.[16] On the basis of these few studies, it seems that a few species dominate the community composition of mangrove avifauna.

In view of the ecological similarities between salt marshes and mangrove forests, we tested the hypothesis that passerines restricted to mangrove forests are similar to tidal-marsh species in having larger bills than their closest nontidal relatives. We investigated passerine species and subspecies that are restricted to mangrove forests throughout the tropics. Rather than restricting our study to one family of birds on one continent (as in the marsh studies), we present a pantropical study that investigates birds from nine families on four continents.[13]

THE DATA

We measured bill morphology, tarsus length, and body mass of 13 mangrove-endemic passerine taxa and their closest putative nontidal relatives through an extensive literature search[13] (Table 1). Mangrove taxa include all resident species and recognized subspecies that occur in mangroves throughout the year. Bill morphology was measured on 10 male specimens, or as close to 10 as possible (see Table 1). We used digital calipers to measure bill depth, bill width, and culmen length (to the closest 0.01 mm) from the anterior edge of the nares. To examine the pattern of covariation in body size and bill size, we also measured tarsus length and obtained a mean body mass for each taxon from the literature. Please see the online Supplementary Material for additional details about material and analytical methods (http://dx.doi.org/10.1525/auk.2011.10262).

RESULTS AND DISCUSSION

The 13 mangrove taxa that we examined had longer bills than their nontidal relatives ($F = 5.51$, df = 1 and 12, $P = 0.03$; Fig. 1). The bills of mangrove taxa were also deeper ($F = 5.29$, df = 1 and 12, $P = 0.04$) than non-mangrove relatives, but they were not wider ($P = 0.13$). Mangrove birds tended to be larger and heavier than their closest nontidal relatives (Fig. 1), but the differences were not significant (paired t-test; tarsus length, $P = 0.17$ and body mass,

TABLE 1. Pairing of endemic tidal mangrove species and putative closest nontidal mangrove relatives, and the number of individuals measured for each species.

Mangrove taxon	Number of individuals measured	Closest nontidal relative	Number of individuals measured
Mangrove Finch (*Camarhynchus heliobates*)	10	Woodpecker Finch (*Camarhynchus pallidus*)	9
Prairie Warbler (*Dendroica discolor paludicola*)	10	Prairie Wabler (*D. discolor*)	10
Yellow "Mangrove" Warbler (*D. petechia erithachorides*)	10	Yellow Warbler (*D. petechia sonoransis*)	10
Mangrove Gerygone (*Gerygone levigaster*)	10	Western Gerygone (*G. fusca*)	10
Large-billed Gerygone (*G. magnirostris magnirostris*)	10	Large-billed Gerygone (*G. magnirostris cairnsensis*)	10
Lemon-breasted Flycatcher (*Microeca flavigaster tormenti*)	8	Lemon-breasted Flycatcher (*M. flavigaster*)	10
Mangrove Blue Flycatcher (*Niltava rufigastra*)	10	Tickell's Blue Flycatcher (*N. tickelliae*)	10
Mangrove Whistler (*Pachycephala cinerea*)	10	White-vented Whistler (*P. albiventris*)	10
White-breasted Whistler (*P. laniodes*)	10	Rufous Whistler (*P. rufiventris*)	10
Mangrove Golden Whistler (*P. melanura*)	10	Golden Whistler (*P. pectoralis*)	6
Mangrove Robin (*Peneoenanthe pulverulaenta*)	10	Blue-gray Robin (*P. cyanus*)	10
Mangrove Pitta (*Pitta megarhyncha*)	3	Blue-winged Pitta (*P. moluccensis*)	10
Yellow White-eye (*Zosterops lutea*)	10	Silvereye (*Z. lateralis*)	10

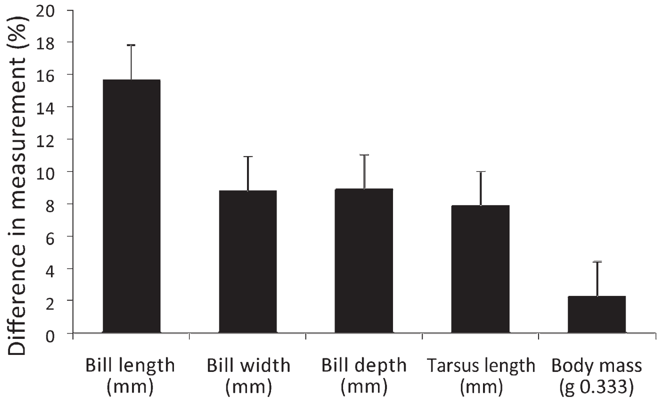

FIG. 1. Mean and standard error of the percentage of difference in bill length, bill width, bill depth, tarsus length, and body mass between mangrove taxa and their closest known relatives: (mangrove – nontidal relative)/nontidal relative × 100.

$P = 0.24$). Therefore, to control statistically for a possible confounding effect of body size in our comparison of mangrove taxa and their relatives, we compared paired species from the two communities using analysis of covariance. Body mass was a significant covariate of bill length ($F = 93.00$, df = 25, $P < 0.01$), and after accounting for this effect, mangrove birds still had longer bills than their non-mangrove relatives ($F = 6.28$, df = 3 and 25, $P = 0.02$; Fig. 2). We also tested for the confounding effect of body mass on bill depth and width and found that body mass, and not habitat, explained the differences in bill depth ($P = 0.22$) and width ($P = 0.52$) in mangrove taxa compared with their closest inland relatives.

Our results reveal a pantropical pattern in which passerine birds endemic to mangrove habitat have evolved longer and deeper bills than their closest nontidal relatives. The results expand upon previous findings that sparrows endemic to the salt marshes of North America have longer and deeper bills than their closest

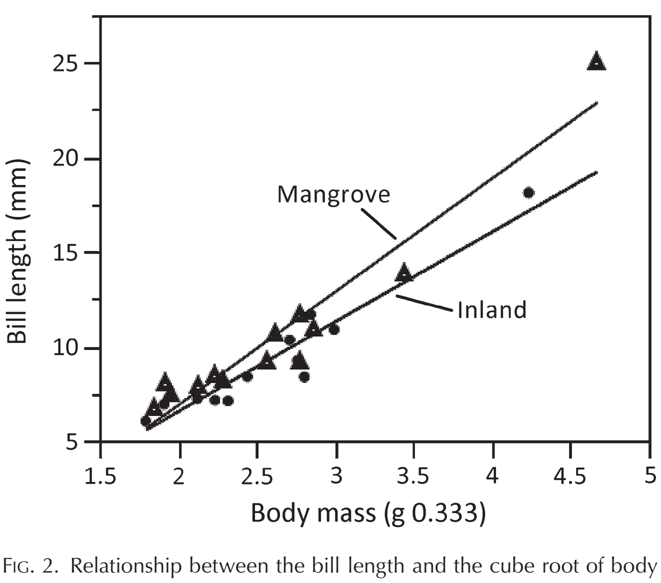

FIG. 2. Relationship between the bill length and the cube root of body mass. Mangrove taxa are represented by triangles, and nontidal relatives are represented by circles.

nontidal relatives.[10] The findings indicate that passerine birds restricted to coastal saline habitats have, in relation to their body size, disproportionately long bills, and that the phenomenon exists as a general ecological rule across continents, much like the patterns that exist among island birds. In addition, the results provide another example, besides salt marshes, of how morphological patterns characteristic of island systems are also found in continental systems.

Our research indicates that longer and deeper bills, but not wider bills, are prevalent in passerine birds restricted to mangrove forests. Body mass and tarsus length did not differ between mangrove species and their nontidal relatives, and thus body size has not driven the observed differences in bill length. Variations in bill size and shape are often indicative of ecological pressures in local environments, especially food resources and foraging behavior.[17] Larger bills, which can also be important in intraspecific conflicts, could also result from more intense intraspecific competition in mangroves than in adjacent terrestrial habitats.[3,9] We suggest that selection on bill length resulting from ecological pressures similar to those found on islands—greater generalization in resource use, increased breeding densities, or both—has driven the difference in bill morphology between mangrove passerines and their closest nontidal relatives.

Sparrows endemic to salt marshes in North America have longer and more slender bills than their closest nontidal relatives,[10] perhaps in part because of a dietary shift from plant materials to arthropods.[18,19,20] Mangrove forests have some food sources that differ from those found in adjacent terrestrial forests.[21,22] Three species of mangrove-restricted birds forage mainly on crabs,[23,24] which are not as abundant in nontidal habitat. However, passerines endemic to mangroves do not exhibit as extreme a shift in diet from that of their nontidal relatives as salt-marsh sparrows do from the diet of their nontidal counterparts. Presumably, this is because both mangrove birds and their closest nontidal relatives are mainly insectivores.[15,16,23]

Longer and more slender bills are correlated with wider foraging-niche breadth.[25] Longer bills are advantageous for probing in small cracks and crevices,[18] where many prey items can be found. Long bills are likely also useful for probing in mud and among mangrove roots where other prey may be abundant. Mangrove endemic birds have very wide foraging-niche breadth.[23,21] In general, mangrove birds are not restricted to specific foraging techniques or a particular stratum of the forest,[15,16,23] and instead have wide foraging niches presumably as a response to the dynamic nature of mangrove environments; mangroves flood twice daily from high tides, which can dramatically change the food availability on and close to the ground. Additionally, depauperate species richness reduces interspecific competition and can lead to an increase in foraging-niche width.[26] Although mangrove-restricted birds are known to have wide foraging niches—and, as we have shown, deep and relatively long bills compared with their closest non-mangrove relatives—no direct comparisons have been made to compare foraging-niche widths or size and diversity of prey use between paired mangrove and non-mangrove species.

An increase in population densities of birds in salt marshes compared with populations in nontidal habitats, as has occurred on islands,[5] could have led to increased sexual selection and subsequent increases in bill size for salt-marsh sparrows.[9] At this time, there are insufficient data to compare population densities of mangrove-restricted taxa and their closest relatives that inhabit inland tropical habitats. Thus, we are unable to determine whether there is a link among population density, increased sexual selection via male–male competition, and bill size. Detailed comparative ecological studies of mangrove and non-mangrove species are needed to determine whether increased population densities are catalysts for the evolution of larger bill sizes in passerines restricted to mangroves.

Larger bills in mangrove-restricted passerines, like in saltmarsh sparrows, might suggest that highly productive continental ecosystems with high population densities and low species richness have ecological and evolutionary processes similar to those found on islands. Future research should be conducted to determine whether the larger bill sizes found in coastal saline habitats, as well as on islands, are a result of foraging behavior, sexual selection, or both.

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