Monkeys on a free-floating island in a Colombian river: further support for over-water colonization

JASON R. ALI*1, UWE FRITZ2, MARIO VARGAS-RAMÍREZ3,4

1 Department of Earth Sciences, University of Hong Kong, Pokfulam Road, Hong Kong (China)
2 Museum of Zoology, Senckenberg Dresden, A. B. Meyer Building, 01109, Dresden (Germany)
3 Roberto Franco Tropical Biology Station, National University of Colombia, Villavicencio (Colombia)
4 Biodiversity and Genetic Conservation, Institute of Genetics, National University of Colombia, Bogotá (Colombia)
* corresponding author, email: jrali@hku.hk

Keywords: Alouatta, Great American Biotic Interchange, long-distance over-water dispersal, New World monkeys, Panama Isthmus, platyrrhines, rafting dispersal.

SUMMARY
Further to the debate associated with the viability of land-bound mammals being able to colonize remote frontiers by way of long-distance over-water dispersal, observations are documented of monkeys (red howlers, Alouatta seniculus) occupying free-standing trees within a large floating island on the Magdalena River in north-west Colombia. Also, we contribute to the discussion related to the 15.0–12.5 Ma (Middle Miocene) arrival of the howler monkeys in Central America, which is well before the Panama Isthmus had fully emerged 3.0–2.8 Ma (Late Pliocene). We speculate it was by way of a raft similar to the ones reported here, possibly from a river entering the sea from northern Colombia.

INTRODUCTION
Practically all of the marine islands host naturally occurring land-locked animals; the small number of exceptions include the Hawaii and Society groups, which are very remote (>3,600 km from the nearest continent) and geologically young (<6 Ma). Where the sea-bed connecting the insular bodies to a mainland has a depth ≤120 m, the general view is that the faunas were assembled due to animals walking in during one of the recent sea-level low-stands associated with a glacial period (over the last 630 ka, the lowest lows in global sea level were
between about 90 and 125 m below the present-day datum; Bintanja et al. 2005). Where the intervening ocean floor is appreciably greater (the average depth of the global ocean is ~3.7 km; Eakins and Sharman 2012), then over-water dispersal is generally invoked, commonly on rafts. Occasionally, though, direct floating is appealed for when the animals are big (e.g. elephants, hippopotamuses; van der Geer et al. 2010, 2015) or have restricted agility (e.g. tortoises; Gerlach et al. 2006). As a consequence, the faunal assemblages on the two sorts of islands are markedly different. With the first (e.g. Bioko, Great Britain, Hainan, Jeju, Taiwan, Tasmania), the suites tend to replicate those on the mainland, with many species, few of which are exclusive to the landmasses (Ali, 2018). With the latter (e.g. Galápagos Archipelago, Madagascar, Mauritis, Seychelles), they are often a highly depleted sub-set comprising hardy, small-bodied organisms, with low energy requirements; some can enter a state of torpor and/or hibernate; endemism is the norm (Ali and Vences, 2019b).

The notion of long-distance over-water dispersal was explored in detail by Matthew (1915) and Simpson (1940), and more recently by Houle (1998, 1999) and de Queiroz (2005, 2014). Recently, however, Mazza et al. (2019) have challenged the idea of mammals colonizing new ground in such a manner. They argue that members of the group are (i) physiologically unsuited to making such trips, (ii) they would have died quickly through starvation and dehydration due to a perceived absence of food and fresh water, and that even if they did survive the crossings then (iii) the genetic bottlenecks associated with a small founder group (gravid individual or a limited number of species members) would make it impossible for the arrivées to establish long-term populations. Ali and Vences (2019a) addressed all three issues and pointed out that the alternative explanation, that is land-bridges, was even more problematic: lack of geological and geophysical evidence corroborating their past existence; such conduits do not strongly filter those taxa that have access to them; colonizations take place over specific periods, and are thus non-randomly distributed through time; movement is bi-directional.

To contribute to the discussion of the over-water dispersal mechanism, we summarize observations made by two of us (MVR and UF) during a December 2016 fieldtrip to northwest Colombia as part of a collaborative effort involving researchers from the Universidad Nacional de Colombia and the Senckenberg Dresden Museum of Zoology. During the visit, which had a herpetological focus, key information was documented for floating islands both on the mid-course of the Magdalena River and in wetlands within the adjoining El Silencio Nature Reserve, at Yondó municipality, Antioquia Department (Fig. 1).

GEOGRAPHICAL AND CLIMATOLOGICAL SETTINGS

The Magdalena is Colombia’s largest river (Restrepo et al. 2006). It extends for 1612 km, with its headwaters located at an altitude of 3685 m above sea level, at the Magdalena ‘lagoon’, with the main part of its course running between the Central and Eastern cordilleras (Fig. 1). The drainage network is geologically young, and appears to have existed since the late Middle Miocene or early Late Miocene (the boundary between the sub-epochs is dated as 11.6 Ma; Walker et al. 2018) and results from tectonic uplift within the northern Andes (Potter 1997, Hoorn et al. 2010, Anderson et al. 2016, Albert et al. 2018). A key feature of the Magdalena’s basin is its vast system of swamps, or ‘ciénagas’; there are around 320,000 such patches, and together they have a maximum flooding area in excess of 12,000 km$^2$ (Rodríguez and Armenteras 2005). Hydrologically, these swamps play a crucial role in buffering the flow of water across the region; ecologically, the shallow-water bodies are important due to their high productivity (Rodríguez and Armenteras 2005).
Figure 1. Map showing the course of the Magdalena River, plus other geographical locations and features that are mentioned in the text. The base image was created using GeoMapApp (Ryan et al. 2009).
The 320 km$^2$ El Silencio Nature Reserve envelopes the Ciénagas de Barbacoas on the Magdalena’s northwest bank. Centred on 6.73N, 74.28W (Fig. 2) are the two large wetlands, Ciénaga Grande (west) and Ciénaga Pequeña (east) that connect with the Magdalena, their surface elevation being c. 90 m (Fig. 2). Within these ciénagas, floating islands are commonplace. They nucleate due to the binding together of submerged and floating aquatic plants including *Eichhornia crassipes* (Mart.) Solms (common water hyacinth), *Ludwigia helminthorrhiza* (Mart.) H. Hara (floating Ludwigia), *Pistia stratiotes* L. (water lettuce), and *Persicaria hydropiperoides* (Michaux) Small (swamp smartweed). As the islands grow and mature, they are then able to harbour large woody vegetation such as *Cecropia peltata* L. (trumpet tree), *Inga* sp. (shimbillo), *Senna reticulata* (Willd.) H. S. Irwin and Barneby (carrion crow bush) and *Euterpe oleracea* Mart. (assai palm) – see Vejarano et al. (2011). During flooding events, rafts from the ciénagas are often flushed out into the Magdalena where they are then carried downstream. An appreciation of the dynamic nature of this flood-plain ecosystem can be gleaned by inspecting the historical imagery for the area that is available on *Google Earth*, the sequence extending back to January 1970.

In terms of the river’s and swamps’ discharge states, it is important to note the two main controls (see Angarita et al. 2018). A base-line pattern caused by the annual overhead migration of the Intertropical Convergence Zone results in two rainy seasons: April to May and September to November; two dry seasons typically last from December to February and July to August. Superimposed on this is the multi-year El Niño-La Niña cycle. During the former, the weather belt is pushed somewhat further to the south than is normal and this creates extended drought conditions across the Magdalena’s basin. In contrast, during the appreciably longer La Niña phases there can be periods of high rainfall that last a year or more, and this can lead to widespread flooding (e.g. Hoyos et al. 2016).

Figure 2. Aerial view of the Magdalena River adjacent to the Ciénagas de Barbacoas where the floating islands were observed. White arrows within the river show the flow direction. The base map is from a *Google Earth* satellite image that was captured on 25 August 2019 (the platform’s archive for this area extends back to 1970).
KEY FIELD OBSERVATIONS

During the aforementioned field excursion, there were multiple instances where on the Magdalena we passed drifting islands sporting upright trees, the tallest of which were about 10 metres, the vegetation mats being typically up to c. 30 m in length, but some >100 m (Fig. 3). Notably, one had some trees whose crowns were occupied by a troop of the local species of howler monkey, *Alouatta seniculus* (Linnaeus, 1766) (red howler monkey). It is likely that the raft had washed out of the Ciénagas de Barbacoas, but it may have been from upriver. Based on the river conditions, the observed animals, probably alongside other species of ground- and tree-dwelling vertebrates, could have travelled a considerable distance downstream. Notably, they would have had an abundance of food, and with no obvious vertical drops or obstructions along the route some of the rafts may have made it to the lower parts of the Magdalena, and potentially out into the open sea. The critical issue is the recording of a small group of same-species land mammals on a floating island in a wide, free-flowing river.

RELATING THE OBSERVATIONS TO THE MIocene PANAMA SEAWAY AND GREAT AMERICAN BIOTIC INTERCHANGE

Developing this further, we note that howler monkeys appear to have originated from their morphologically similar ancestor *Stirtonia tatacoensis* (Stirton, 1951) that existed in what is now the upper reaches of the Magdalena River basin (Stirton 1951, Hershkovitz 1970, Fleagle et al. 1997, Rosenberger et al. 2015). Doyle et al. (2021) hypothesized that howlers from northwest South America crossed into Central America 13.2 Ma (12.5–15.0 Ma) by way of the Panama Isthmus. There is, however, a major problem with this idea because a truly unbroken causeway between South and Central America has only existed since about 3 Ma (Late Pliocene; Coates & Stallard 2013, O’Dea et al. 2016). Subsequently, there was a massive transfer of land-locked species between the two areas, an event that is known as the Great American Biotic Interchange (Marshall 1988, Woodbourne 2010; see also Simpson 1950). To this end, we propose an alternative explanation to the one of Doyle et al. (2021) that involved *Alouatta* colonizing Mesoamerica by way of a floating island similar to those described above. Acknowledging the uncertainties in the Magdalena River’s age of genesis, it is just possible that such a raft departed its mouth in north-west South America close to the Middle Miocene-Late Miocene boundary. In support of this argument attention is drawn to the remote sensing study of Moreno-Madriñán et al. (2015) in which they mapped the pathways of suspended sediment exiting the mouth of the Magdalena. Notably, a sizable fraction of the material is picked up by the Caribbean Current and swept west toward Panama (also see Fig. 1).

CONCLUSIONS

We have provided new information related to the feasibility of over-water dispersal to explain how some land-bound vertebrates have colonized remote locations. Specifically, it involved summarizing observations of a group of medium-sized mammals atop upright trees that were being carried downriver on a floating island in north-west Colombia. Also, we have added to the debate related to the transfer of land animals between the Americas prior to the formation of a fully-connected Panama Isthmus causeway. Finally, we note that if ancestors of the platyrhine monkeys colonized the Americas by way of a raft that departed Africa in the Middle Eocene (Silvestro et al. 2019), then a Miocene journey by some of their descendants from northwest South America to Central America might in comparison be regarded as being almost inconsequential.
Figure 3. Photograph of one of the floating islands on the Magdalena River during the December 2016 fieldtrip (credit UF). As a scale guide, the raft is about 80 m across. Also note that O’Dea et al. (2016) includes video footage from 2010 of similar scale rafts travelling down the Chagres River in Panama.
REFERENCES

Albert, J. S., Val, P. & Hoorn, C. (2018) The changing course of the Amazon River in the Neogene: center stage for Neotropical diversification. Neotropical Ichthyology, 16(3), e180033. DOI: 10.1590/1982-0224-20180033

Ali, J. R. (2018) Islands as biological substrates: continental. Journal of Biogeography, 45(5), 1003–1018. DOI: 10.1111/jbi.13186

Ali, J. R. & Vences, M. (2019a) Mammals and long-distance over-water colonization: the case for rafting dispersal; the case against phantom causeways. Journal of Biogeography, 46(11), 2632–2636. DOI: 10.1111/jbi.13659

Ali, J. R. & Vences, M. (2019b) Novel summary metrics for insular biotic assemblages based on taxonomy and phylogeny: biogeographical, palaeogeographical and possible conservational applications. Journal of Biogeography, 46(12), 2735–2751. DOI: 10.1111/jbi.13706

Anderson, V. J., Horton, B. K., Saylor, J. E., Mora, A., Tesón, E., Breecker, D. O. & Ketcham, R. A. (2016) Andean topographic growth and basement uplift in southern Colombia: implications for the evolution of the Magdalena, Orinoco, and Amazon river systems. Geosphere, 12(4), 1235–1256. DOI: 10.1130/GES01294.1

Angarita, H., Wickel, A. J., Sieber, J., Chavarro, J., Maldonado-Ocampo, J. A., Herrera-R, G. A., Delgado, J. & Purkey, D. (2018) Basin-scale impacts of hydropower development on the Mompós Depression wetlands, Colombia. Hydrology and Earth System Sciences, 22(5), 2839–2865. DOI: 10.5194/hess-22-2839-2018

Bintanja, R., van de Wal, R. S. W. & Oerlemans, J. (2005) Modelled atmospheric temperatures and global sea level over the past million years. Nature, 437(7055), 125–128. DOI: 10.1038/nature03975

Coates, A. G. & Stallard, R. F. (2013) How old is the Isthmus of Panama? Bulletin of Marine Science, 89(4), 801–813. DOI: 10.5343/bms.2012.1076

de Queiroz, A. (2005) The resurrection of oceanic dispersal in historical biogeography. Trends in Ecology and Evolution, 20(2), 68–73. DOI: 10.1016/j.tree.2004.11.006

de Queiroz, A. (2014) The Monkey’s Voyage: How Improbable Journeys Shaped the History of Life. Basic Books, New York.

Doyle, E. D., Prates, I., Sampaio, I., Koiffmann, C., Silva, W. A., Carnaval, A. C. & Harris, E. E. (2021) Molecular phylogenetic inference of the howler monkey radiation (Primates: Alouatta). Primates, 62(1), 177–188. DOI: 10.1007/s10329-020-00854-x.

Eakins, B. W. & Sharman G. F. (2012) Hypsographic Curve of Earth’s Surface from ETOPO1. NOAA National Geophysical Data Center, Boulder, CO.

Fleagle, J. G., Kay, R. F. & Anthony, M. R. L. (1997) Fossil New World monkeys. In: Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia (ed. by R. F. Kay, R. H. Madden, R. L. Cifelli, J. J. Flynn), pp 473–495. Smithsonian Institution Press, Washington.

Gerlach, J., Muir, C. & Richmond, M. D. (2006) The first substantiated case of trans-oceanic tortoise dispersal. Journal of Natural History, 40(41–43), 2403–2408. DOI: 10.1080/00222930601058290

Hoorn, C. M., Wesselingh, F. P., Ter Steege, H., et al. (2010) Amazonia through time: Andean uplift climate change, landscape evolution and biodiversity. Science, 330 (6006), 927–931. DOI: 10.1126/science.1194585

Houle, A. (1998) Floating islands: a mode of long-distance dispersal for small to medium-sized terrestrial vertebrates. Diversity and Distributions, 4(5–6), 201–216.

Houle, A. (1999) The origin of Platyrrhines: an evaluation of the Antarctic scenario and the Floating island model. American Journal of Physical Anthropology, 109(4), 541–559. DOI: 10.1002/(SICI)1096-8644(19998)109:4<541::AI

Hoyos, N., Escobar, J., Restrepo, J., Arango, A. & Ortiz, J. (2013) Impact of the 2010 and 2011 La Niña phenomenon in Colombia, South America: the human toll of an extreme weather event. Applied Geography, 39(1), 16–25. DOI: 10.1016/J.APGEOG.2012.11.018

Marshall, L. G. (1988) Land Mammals and the Great American Interchange. American Scientist, 76(4), 380–388.

Matthew, W. D. (1915) Climate and evolution. Annals of the New York Academy of Sciences, 24(1), 171–318.

Mazza, P. P. A., Buccianti, A. & Savorelli, A. (2019) Grasping at straws: a re-evaluation of sweepstakes colonisation of islands by mammals.
Biological Reviews, 94(4), 1364–1380. DOI: 10.1111/brv.12506

Moreno-Madriñán, M. J., Rickman, D. L., Ogashawara, I., Irwin, D. E., Yee, J. & Al-Hamdan, M. Z. (2015) Using remote sensing to monitor the influence of river discharge on watershed outlets and adjacent coral Reefs: Magdalena River and Rosario Islands, Colombia. International Journal of Applied Earth Observation and Geoinformation, 38(1), 204–215. DOI: 10.1016/j.jag.2015.01.008

O’Dea A., Lessios, H. A., Coates, A. G., et al. (2016) Formation of the Isthmus of Panama. Science Advances, 2(8), e1600883. DOI: 10.1126/sciadv.1600883

Potter, P. E. (1997) The Mesozoic and Cenozoic paleodrainage of South America: a natural history. Journal of South American Earth Sciences, 10(5–6), 331–344. DOI: 10.1016/S0895-9811(97)00031-X

Restrepo, J. D., Kjerfve, B., Hermelin, M. & Restrepo, J. C. (2006) Factors controlling sediment yield in a major South American drainage basin: the Magdalena River, Colombia. Journal of Hydrology, 316(1–4), 213–232. DOI: 10.1016/B978-0-12-374711-2.01117-7

Rodríguez, N. & Armenteras, D. (2005) Ecosistemas naturales de la cuenca del Río Magdalena. In: Los sedimentos del Río Magdalena: Reflejo de la Crisis Ambiental (ed. by J. D. Restrepo-Angel), pp 79–98. Medellin: Editorial Universidad EAFIT.

Rosenberger, A. L., Cooke, S. B., Halenar, L. B., Tejedor, M. F., Hartwig, W. C., Novo, N. M. & Muñoz-Saba, Y. (2015) Fossil alouattines and the origins of Alouatta: craniodental diversity and interrelationships. In: Howler Monkeys. Developments in Primatology: Progress and Prospects (ed. by M. Kowalewski, P. Garber, L. Cortés-Ortiz, B. Urbani, D. Youlatos), pp 21–54. Springer, New York. DOI: 10.1007/978-1-4939-1957-4_2

Ryan, W. B. F., Carbotte, S. M., Coplan, J. O., et al. (2009) Global multi-resolution topography synthesis. Geochemistry, Geophysics, Geosystems, 10(3), Q03014. DOI: 10.1029/2008GC002332

Silvestro, D., Tejedor, M. F., Serrano-Serrano, M. L., et al. (2019) Early arrival and climatically-linked geographic expansion of New World monkeys from tiny African ancestors. Systematic Biology, 68(1), 78–92. DOI: 10.1093/sysbio/syy046

Simpson, G. G. (1940) Mammals and land bridges. Journal of the Washington Academy of Science, 30(4), 137–163.

Simpson, G. G. (1950) History of the fauna of Latin America. American Scientist, 38(3), 361–389.

Stirton, R. A. (1951) Ceboid monkeys from the Miocene of Colombia. Berkeley, University of California Publication, Bulletin of the Department of Geological Sciences, 28, 315–356.

c van der Geer, A., Lyras, G., de Vos, J. & Dermitzakis, M. (2010) Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Islands. John Wiley & Sons, Chichester.

c van der Geer, A. A. E., Anastasakis, G. & Lyras, G. A. (2015) If hippopotamuses cannot swim, how did they colonize islands: a reply to Mazza. Lethaia, 48(3), 147–150. DOI: 0.1111/let.12074

Vejarano, S., Arbeláez, F., Henández, M., et al. (2011) Actualización al plan de manejo ambiental del complejo cenagoso de Narbacoas, Municipio de Yondó, Antioquia. Fundación Biodiversa Colombia. Final report, 63 pp.

Walker, J. D., Geissman, J. W., Bowring, S. A. & Babcock, L. E. (compilers) 2018. Geologic Time Scale v. 5.0. Geological Society of America. DOI: 10.1130/2018.CTS005R3C.

Woodburne, M. O. (2010) The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. Journal of Mammalian Evolution, 17(4), 245–264. DOI: 10.1007/s10914-010-9144-8

Submitted: 4 February 2021
First decision: 31 March 2021
Accepted: 7 May 2021
Edited by Francesco Maria Angelici