UC Berkeley

UC Berkeley Previously Published Works

Title

Long-distance dispersal over land by fishes: extremely rare ecological events become probable over millennial timescales

Permalink

https://escholarship.org/uc/item/39b6c0cm

Journal

Proceedings of the Royal Society B, 285(1881)

ISSN

0962-8452

Authors

Martin, Christopher H
Turner, Bruce J

Publication Date

2018-06-27

DOI

10.1098/rspb.2017.2436

Peer reviewed

eScholarship.org Powered by the California Digital Library
University of California

Downloaded from http://rspb.royalsocietypublishing.org/ on November 7, 2018

PROCEEDINGS B

rspb.royalsocietypublishing.org

Invited reply

Cite this article: Martin CH, Turner BJ. 2018 Long-distance dispersal over land by fishes: extremely rare ecological events become probable over millennial timescales. *Proc. R. Soc. B* **285**: 20172436. http://dx.doi.org/10.1098/rspb.2017.2436

Received: 31 October 2017
Accepted: 23 May 2018

Subject Category:
Evolution

Subject Areas:
ecology, evolution

Author for correspondence:
Christopher H. Martin
e-mail: chmartin@unc.edu

The accompanying comment can be viewed at http://dx.doi.org/10.1098/rspb.2017.1648.

THE ROYAL SOCIETY PUBLISHING

Long-distance dispersal over land by fishes: extremely rare ecological events become probable over millennial timescales

Christopher H. Martin[1] and Bruce J. Turner[2]

[1]Department of Biology, University of North Carolina at Chapel Hill, NC 27599, USA
[2]Department of Biological Sciences, Virginia Tech, VA, USA

CHM, 0000-0001-7989-9124

1. Introduction

Our recent coalescent estimate for the time of colonization of Devil's Hole by *Cyprinodon* pupfish challenged deeply held and widespread assumptions about this species based only on a poor fossil record and a geological calibration from the Middle East [1,2]. Our genome-wide analyses estimated a recent age for the Devil's Hole pupfish (DHP), *Cyprinodon diabolis*, within the past 105–830 years and frequent gene flow among Death Valley populations [1]. This estimate depends, in turn, on a good estimate of the pupfish mutation rate. We estimated this indirectly from the *Cyprinodon* substitution rate, and vertebrate mutation rates are known to vary over at least an order of magnitude [3,4]. However, our initial approach using a time-calibrated phylogenetic concatenated analysis cannot overestimate the rate by more than twofold relative to a gene tree analysis [5]. Furthermore, the unique natural history of DHP—including its miniscule population size, short lifespan, small adult size, high metabolic rate, high environmental temperature and high environmental stressors—all predict a higher mutation rate in this species. Except for their larger effective population sizes [6], this likely applies to *Cyprinodon* pupfishes in general [3–5,7]. We argue that DHP is a prime candidate for exhibiting one of the highest vertebrate mutation rates known [5] and should be further investigated using the gold standard of pedigree sequencing [8,9]. We further argue that a young age for this species does not decrease its conservation value but enhances it due to the evolution of such a unique life history and phenotype in a remarkably short time period.

Knott *et al*. (KEA) [10] do not dispute this young age for DHP, but rather the resulting divergence time estimates for *Cyprinodon* as a whole and its dispersal across North America in the past 25 thousand years (kya) [1]. These ages were based on our internal calibration of the stem age of the Laguna Chichancanab pupfish adaptive radiation to 8 kya, based on fossil evidence and isotopic analyses of multiple cores that indicated that the lake basin was dry prior to that time point [11]. One concern is that this very recent calibration is only appropriate for estimating recent divergent events on the same timescale [12]. Owing to the long-term effects of purifying selection and potentially other forces, the substitution rate over longer time periods (tens to hundreds of thousands of years) is almost certainly slower than the spontaneous mutation rate in each generation [13,14]. Thus, the age of *Cyprinodon* as a whole is almost certainly older than estimated by our time-calibrated phylogenetic analysis based on a recent geological event. This relationship should scale with effective population size as well as other demographic factors (e.g. population bottlenecks [6]) through time, so it is difficult to say exactly how much older *Cyprinodon* may be [15]. We also cannot rule out the possibility that the Chichancanab stem lineage is much older than the endemic basin in which it occurs. However, we originally argued that this is unlikely given the inability of these trophic specialist species to coexist with widespread native Yucatan species such as *Astyanax fasciatus*

© 2018 The Author(s) Published by the Royal Society. All rights reserved.

Downloaded from http://rspb.royalsocietypublishing.org/ on November 7, 2018

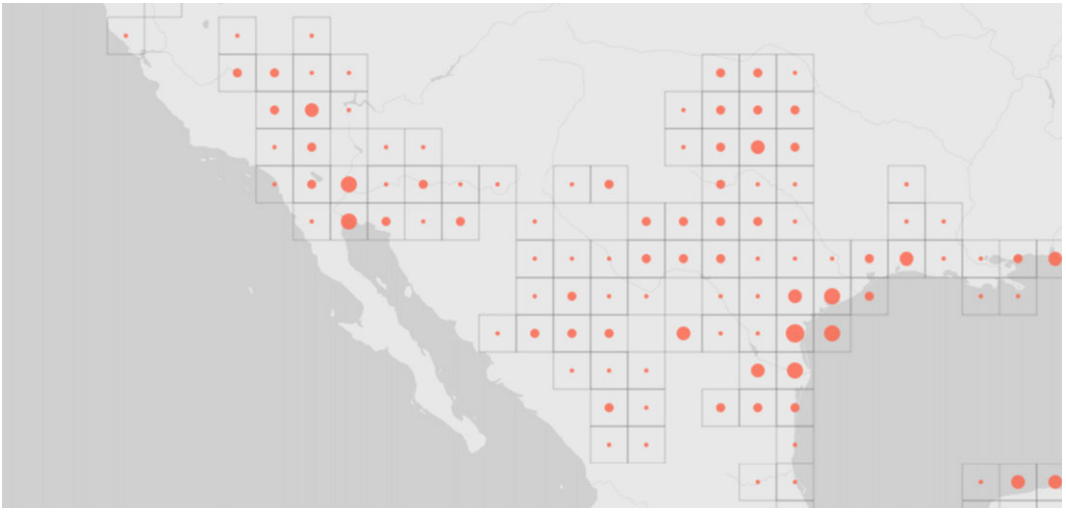

Figure 1. Global Biological Information Facility data for *Cyprinodon* species occurrences within each grid throughout the North American southwest, from the Gulf of Mexico to Death Valley. Note the current widespread occurrences from the Rio Grande to the Gila River and Death Valley drainage basins.

[1,16]. There are also no other isolated brackish lakes known from this region to provide a suitable habitat.

Instead of discussing these legitimate concerns, KEA take the position that all fish require a waterway to disperse, no matter the timescale. They assert that pupfish required a waterway in the last 25 kya connecting the Gulf of Mexico with the Great Basin of California to disperse this far inland. This was specifically questioned by Echelle [17] based on available phylogenetic evidence consistent with our recent study; geological hypotheses that no connections existed between these basins should also be examined (see Discussion below). The broader position that fish dispersal over land is impossible has been refuted countless times, beginning with Darwin, who conducted famous experiments on the ability of aquatic organisms (snails, seeds and plants) to be transported over land by bird vectors. For example, his most famous experiment involved dipping dried duck's feet into an aquarium containing aquatic snails and documenting that they survived out of water for up to 20 h. In the *Origin*, he concluded that 'a duck or heron might fly at least 600 or 700 miles, and would be sure to alight on a pool or rivulet' [18,19]. He did not personally conduct experiments with fish eggs, but corresponded with Sir Humphry Davy who experimented with how long fertilized salmon eggs remained viable after exposure to air, and reported that even a small fish (char) could survive for 72 h barely covered with water [18]. Darwin considered this so important that he made sure it was published by the Royal Society [18,20]. He also collected observations of aquatic animals found on bird's feet in nature throughout his later career, resulting in his final publication [21]. Indeed, given the effort he and colleagues obviously expended on these studies, Darwin certainly would have been quite surprised by KEA's claim that Darwin 'concluded' that aquatic organisms never dispersed long distances over land.

KEA's emphasis on the 3000 km distance from the Gulf of Mexico to Death Valley is misleading. The relevant distance is *between drainage basins*; it should be obvious that fish can swim up rivers because pupfishes have done this throughout their range (figure 1) [22]. For example, the distance between tributaries for one of the proposed routes from the Rio Grande to the Gila River basin is less than 130 km. These mountain passes lie within the flyways of numerous aquatic birds and well within Darwin's proposed range of 600 miles. Furthermore, pupfish eggs are 1–2 mm in diameter and are repeatedly deposited by the female in aquatic plants, algae mats or fine sand/silt [23–25]. They adhere to these plants or fine mud and are desiccation resistant, like those of most cyprinodontiform fishes, a group in which drought-resistant embryonic diapause has repeatedly evolved [26]. 25 kya is a long time; it is wondrous, though not difficult, for us to imagine rare millennial events such as a duck transporting a few eggs stuck to its webbed feet, which maintain a humid environment when tucked into its body during flight [18].

The geological record of ancient inter-basin connections cannot completely account for the observed phylogenetic relationships among Western pupfishes. This is not a novel conclusion of our paper, but has been evident for some time. For example, in a detailed reanalysis of mtDNA sequence divergences, Echelle (pg. 28) noted that 'there is a general paucity of geological support for the inter-basin connections inferred from this study. *This indicates that dispersal across basin divides might have played a greater role than anticipated for the historical biogeography of the group*' (emphasis added). The discrepancy is important because pupfishes 'primarily occupy springs and low-gradient streams on valley floors,' habitats that 'are more likely to reflect geological history than are [those] of most other fish groups in the region' [17]. Thus, 'either our knowledge of (Neogene surface-water connections) is incomplete or pupfish dispersal across basin divides via small, relatively transient, surface-water connections have been more common than expected based on. . .habitats generally occupied by this group' [17]. 'Dispersal could have been facilitated by headwater stream captures or transient flow across basin divides during extreme rainfall episodes' [17, p. 34]. While Echelle did not consider overland dispersal, the potential explanation we propose, nothing in his analysis precludes this possibility. In any case, KEA to the contrary, there appears to be little argument that non-hydrographic factors likely have been involved in shaping the historical distribution of Western pupfishes.

There are, in fact, numerous examples of isolated water bodies colonized by fishes through long-distance dispersal

Downloaded from http://rspb.royalsocietypublishing.org/ on November 7, 2018

over land, including nearly a hundred volcanic crater lake fish species flocks [27–34], all bolide craters [35] and thousands of endorheic lake basins (e.g. [22,36,37]). For example, 18% of the world's landmass drains into endorheic lake basins [38,39]. The most relevant of these is Devil's Hole itself, which was apparently never connected to the surrounding Amargosa River basin in its entire 60 kya history [40]. Similarly, Laguna Chichancanab is an endorheic basin which was never connected to other water bodies; this is also the case for the habitats of several other desert pupfish species [36,41]. We have also personally searched over 30 hypersaline endorheic lake basins across eight islands in the Bahamian archipelago and found pupfish in nearly every lake with salinities below 50 ppt (CH Martin, personal observations 2011, 2013, 2018; [42]). There is also strong circumstantial evidence of trans-oceanic dispersal by cichlid and cyprinodontiform fishes [42–46], which is perhaps more remarkable than over land dispersal across kilometres of desert. Finally, several alternative mechanisms of fish dispersal have been directly documented, including human introductions, stream capture events and water spouts [47]. Indeed, just a few months ago it rained fishes in Mexico [48]. We agree that fish primarily colonize lakes and rivers via waterways; our point is that there are rare exceptions to this rule.

Finally, we disagree with KEA's claim that a process must be directly observed by humans to be invoked as a potential explanation. Instead, we argue that long-distance dispersal of fishes and their eggs over land is plausible and has repeatedly occurred all over the world.

Data accessibility. This study contains no associated data.

Authors' contributions. C.M. wrote the manuscript. B.J.T. revised and commented on it. Both authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. We received no funding for this study.

References

1. Martin CH, Crawford JE, Turner BJ, Simons LH. 2016 Diabolical survival in death valley: recent pupfish colonization, gene flow, and genetic assimilation in the smallest species range on earth. *Proc. R. Soc. B* **283**, 20152334. (doi:10.1098/rspb.2015.2334)
2. Reed J, Stockwell C. 2014 Evaluating an icon of population persistence: the Devil's Hole pupfish. *Proc. R. Soc. B* **281**, 1648–1658. (doi:10.1098/rspb.2014.1648)
3. Lynch M. 2010 Evolution of the mutation rate. *Trends Genet.* **26**, 345–352.
4. Bromham L. 2009 Why do species vary in their rate of molecular evolution? *Biol. Lett.* **5**, 401–404. (doi:10.1098/rsbl.2009.0136)
5. Martin C, Hohna S, Crawford J, Turner B, Richards E, Simons L. 2017 The complex effects of demographic history on the estimation of substitution rate: concatenated gene analysis results in no more than twofold overestimation. *Proc. R. Soc. B* **284**, 20170537. (doi:10.1098/rspb.2017.0537)
6. McGirr JA, Martin CH. 2016 Novel candidate genes underlying extreme trophic specialization in Caribbean pupfishes. *Mol. Biol. Evol.* **34**, 873–888.
7. Martin C, Hohna S. 2017 New evidence for the recent divergence of Devil's Hole pupfish and the plausibility of elevated mutation rates in endangered taxa. *Mol. Ecol.* 27, 831–838.
8. Harris K. 2015 Evidence for recent, population-specific evolution of the human mutation rate. *Proc. Natl Acad. Sci. USA* **112**, 3439–3444. (doi:10.1073/pnas.1418652112)
9. Smeds L, Qvarnstrom A, Ellegren H. 2016 Direct estimate of the rate of germline mutation in a bird. *Genome Res.* **26**, 1211–1218. (doi:10.1101/gr.204669.116)
10. Knott J, Phillips F, Eheis M, Sada D, Jayko A, Axen G. 2018 Geologic and hydrologic concerns about pupfish divergence during the last glacial maximum. *Proc. R. Soc. B* **285**, 20171648.
11. Hodell D, Curtis J, Brenner M. 1995 Possible role of climate in the collapse of Classic Maya civilization. *Nature* **375**, 391–394. (doi:10.1038/375391a0)
12. Ho SYW, Phillips MJ. 2009 Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Syst. Biol.* **58**, 367–380. (doi:10.1093/sysbio/syp035)
13. Ho SYW, Phillips MJ, Cooper A, Drummond AJ. 2005 Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. *Mol. Biol. Evol.* **22**, 1561–1568. (doi:10.1093/molbev/msi145)
14. Ho SYW, Lanfear R, Bromham L, Phillips MJ, Soubrier J, Rodrigo AG, Cooper A. 2011 Time-dependent rates of molecular evolution. *Mol. Ecol.* **20**, 3087–3101. (doi:10.1111/j.1365-294X.2011.05178.x)
15. Woodhams M. 2006 Can deleterious mutations explain the time dependency of molecular rate estimates? *Mol. Biol. Evol.* **23**, 2271–2273. (doi:10.1093/molbev/msl107)
16. Strecker U. 2006 The impact of invasive fish on an endemic *Cyprinodon* species flock (Teleostei) from Laguna Chichancanab, Yucatan, Mexico. *Ecol. Freshw. Fish* **15**, 408–418. (doi:10.1111/j.1600-0633.2006.00159.x)
17. Echelle A. 2008 The western North American pupfish clade (Cyprinodontidae: Cyprinodon): mitochondrial DNA divergence and drainage history. *Geol. Soc. Am. Spec. Pap.* **439**, 27–38.
18. Costa J. 2017 *Darwin's backyard: how small experiments led to a big theory*. New York, NY: Norton and Company, Inc.
19. Darwin C. 1859 *The origin of species by means of natural selection: or, the preservation of favored races in the struggle for life*. London, UK: Murray.
20. Davy H. 1856 On the ova of salmon. *Phil. Trans. R. Soc. Lond. B* **146**, 21–29. (doi:10.1098/rstl.1856.0005)
21. Darwin C. 1882 On the dispersal of freshwater bivalves. *Nature* **25**, 529–530. (doi:10.1038/025529f0)
22. Martin CH, Wainwright PC. 2011 Trophic novelty is linked to exceptional rates of morphological diversification in two adaptive radiations of *Cyprinodon* pupfishes. *Evolution* **65**, 2197–2212. (doi:10.1111/j.1558-5646.2011.01294.x)
23. Martin CH, Wainwright PC. 2013 Multiple fitness peaks on the adaptive landscape drive adaptive radiation in the wild. *Science* **339**, 208–211. (doi:10.1126/science.1227710)
24. Martin CH, Wainwright PC. 2013 A remarkable species flock of *Cyprinodon* pupfishes endemic to San Salvador Island, Bahamas. *Bull. Peabody Museum Nat. Hist.* **54**, 231–240. (doi:10.3374/014.054.0201)
25. Martin CH. 2016 Context-dependence in complex adaptive landscapes: frequency and trait-dependent selection surfaces within an adaptive radiation of Caribbean pupfishes. *Evolution* **70**, 1265–1282.
26. Furness AI, Reznick DN, Springer MS, Meredith RW. 2015 Convergent evolution of alternative developmental trajectories associated with diapause in African and South American killifish. *Proc. R. Soc. B* **282**, 20142189. (doi:10.1098/rspb.2014.2189)
27. Martin CH. 2012 Weak disruptive selection and incomplete phenotypic divergence in two classic examples of sympatric speciation: Cameroon crater lake cichlids. *Am. Nat.* **180**, E90–E109. (doi:10.1086/667586)
28. Martin CH. 2013 Strong assortative mating by diet, color, size, and morphology but limited progress toward sympatric speciation in a classic example: Cameroon crater lake cichlids. *Evolution* **67**, 2114–2123.
29. Martin CH, Cutler JS, Friel JP, Dening T, Coop G, Wainwright PC. 2015 Complex histories of repeated colonization and hybridization cast doubt on the clearest examples of sympatric speciation in the wild. *Evolution* **69**, 1406–1422.
30. Kautt AF, Machado-Schiaffino G, Meyer A. 2016 Multispecies outcomes of sympatric speciation after admixture with the source population in two radiations of Nicaraguan Crater Lake Cichlids. *PLoS*

Downloaded from http://rspb.royalsocietypublishing.org/ on November 7, 2018

Genet. **12**, e1006157. (doi:10.1371/journal.pgen.1006157)

31. Malinsky M *et al*. 2015 Genomic islands of speciation separate cichlid ecomorphs in an East African crater lake. *Science* **350**, 1493–1498. (doi:10.1126/science.aac9927)
32. Wagner CE, Harmon LJ, Seehausen O. 2012 Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* **487**, 366–370.
33. Poelstra J, Richards E, Martin C. 2018 Speciation in sympatry with ongoing secondary gene flow and an olfactory trigger in a radiation of Cameroon cichlids. *bioRxiv*. (doi:10.1101/229864)
34. Richards E, Poelstra J, Martin C. 2017 Don't throw out the sympatric species with the crater lake water: fine-scale investigation of introgression provides weak support for functional role of secondary gene flow in one of the clearest examples of sympatric speciation. *bioRxiv*. (doi:10.1101/217984)
35. Stager J, Alton K, Martin C, King D, Petruny L, Wiltse B, Livingstone D. 2017 On the age and origin of Lake Ejagham, Cameroon, and its endemic fishes. *Quat. Res.* **89**, 1–12.
36. Humphries J, Miller RR. 1981 A remarkable species flock of pupfishes, genus *Cyprinodon*, from Yucatan, Mexico. *Copeia* **1981**, 52–64. (doi:10.2307/1444040)
37. Kalk MJ, Schulten-Senden CM. 1977 Zooplankton in a tropical endorheic lake (Lake Chilwa, Malawi) during drying and recovery phases. *J. Limnol. Soc. South. Africa* **3**, 1–7. (doi:10.1080/03779688.1977.9632922)
38. 2008 Endorheic Lakes: Waterbodies that don't flow to the sea. *United Nations Environ. Program*.
39. Hammer U. 1986 *Saline lake ecosystems of the world*. Berlin, Germany: Springer.
40. Riggs A, Deacon J. 2002 Connectivity in desert aquatic ecosystems: the devils hole story. *Spring-fed Wetl. Important Sci. Cult. Resour. Intermt. Reg.* **11**, 1–38.
41. Contreras-Balderas S, Almada-Villela P. 1996 *Cyprinodon alvarezi*. The IUCN Red List of Threatened Species. See www.iucnredlist.org.
42. Martin CH. 2016 The cryptic origins of evolutionary novelty: 1000-fold faster trophic diversification rates without increased ecological opportunity or hybrid swarm. *Evolution* **70**, 2504–2519.
43. Friedman M, Keck BP, Dornburg A, Eytan RI, Martin CH, Hulsey CD, Wainwright PC, Near TJ. 2013 Molecular and fossil evidence place the origin of cichlid fishes long after Gondwanan rifting. *Proc. R. Soc. B* **280**, 20131733. (doi:10.1098/rspb.2013.1733)
44. Richards E, Martin C. 2017 Adaptive introgression from distant Caribbean islands contributed to the diversification of a microendemic radiation of trophic specialist pupfishes. *PLoS Genet.* **13**, e1006919. (doi:10.1371/journal.pgen.1006919)
45. Martin CH, Feinstein LC. 2014 Novel trophic niches drive variable progress towards ecological speciation within an adaptive radiation of pupfishes. *Mol. Ecol.* **23**, 1846–1862. (doi:10.1111/mec.12658)
46. Haney RA, Turner BJ, Rand DM. 2009 A cryptic lineage within the pupfish *Cyprinodon dearborni* suggests multiple colonizations of South America. *J. Fish Biol.* **75**, 1108–1114. (doi:10.1111/j.1095-8649.2009.02378.x)
47. Strange RM. 1998 Mitochondrial DNA variation in johnny darters (Pisces: Percidae) from eastern Kentucky supports stream capture for the origin of upper Cumberland river fishes. *Am. Midl. Nat.* **140**, 96–102. (doi:10.1674/0003-0031(1998)140[0096:MDVIJD]2.0.CO;2)
48. 2017 Fish fall from sky with rain in northern Mexico. *CBC News*., The Associated Press. See http://www.cbc.ca/news/world/its-raining-fish-1.4310791.