

## LETTER TO THE EDITOR

# A response to Hoelzel & Moura

Heredity (2017) 118, 511–512; doi:10.1038/hdy.2016.118; published online 7 December 2016

In their phylogeography study published in *Heredity*, Moura *et al.* (2015) used an approach that treats geographic distribution as a trait of the taxa at the tips of a phylogenetic tree and estimates the most likely ancestral state of this trait at each node. From this they concluded that the ‘resident’ fish-eating and ‘transient’ mammal-eating killer whale ecotypes diverged in sympatry from a common ancestor that inhabited the North Pacific. In our comment (Foote and Morin, 2015) we questioned whether this approach was robust for inter-population comparisons, and our reanalysis of their data (Foote and Morin, 2016) found that these sympatric killer whale ecotypes have more complex evolutionary histories than can be modelled by a simple bifurcating tree.

In their Letter to the Editor, Hoelzel and Moura (hereafter H&M) provide no new arguments or evidence in support of the central conclusion of their 2015 study: that North Pacific killer whale ecotypes arose from primary divergence-with-gene-flow. Instead, H&M reiterate their hypothesis that differences in spatial and temporal use of habitat linked to foraging specialisation drive divergence of sympatric killer whale ecotypes. We don’t contest that this mechanism may maintain reproductive isolation between killer whale ecotypes. That was not the focus of our paper. To avoid further repetition, we direct the reader to our recently published comment (Foote and Morin, 2015) and paper (Foote and Morin, 2016) and the suite of analyses therein. These provide a detailed rationale and statistical support for our assertion that the evolutionary history of ecotype formation among North Pacific killer whales is complex and that evidence for primary sympatric divergence is equivocal.

We take this opportunity to address several statements in H&M’s Letter to the Editor, which we believe are misleading.

From H&M (2016):

*“They investigate these poorly resolved relationships in some detail using the  $f_4$  statistic to distinguish between admixture and incomplete lineage sorting. However, each bootstrapped comparison is based on just five SNPs, so power is low...”*

This is incorrect; the  $f_4$  statistic was estimated using 2316 SNPs, standard error was estimated using jackknife resampling: repeated estimation of the  $f_4$  statistic over 461 blocks of five adjacent SNPs, systematically removing a different block of five adjacent SNPs for each estimate. We repeated this for different block sizes, to assess the effect on the standard error and Z-score (see Table S4 of Foote and Morin, 2016).

From H&M (2016):

*“Foote and Morin (2016) emphasise the importance of the North Atlantic population in support of their conclusions, however, our ABC modelling analyses that included the North Atlantic (H&M, 2015)*

*supported the topology presented in our nuclear consensus phylogeny (Moura *et al.*, 2015)”*.

H&M (2015) did not present the results of ABC modelling analyses that included the North Atlantic population. See Figure 1 in H&M (2015).

From H&M (2016):

*“For example, they suggest gene flow between transient and resident populations in the North Pacific (consistent with our data from Hoelzel *et al.* (2007) and Moura *et al.* (2014a)). We note that the broader implications from the reticulate gene flow we have each described may be inconsistent with earlier proposals for multiple killer whale species (for example, Morin *et al.*, 2010), though this can also occur among established species.”*

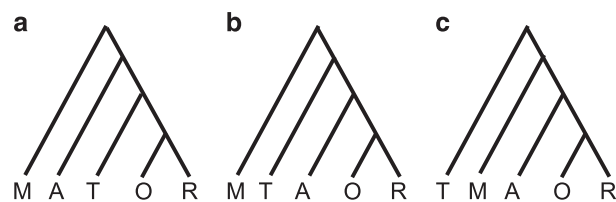
This is only partially true; the  $f_4$  statistics and TreeMix graph presented in Foote and Morin (2016) are consistent with ancestral admixture, and do not require (or rule out) recent or ongoing gene flow. Our STRUCTURE analysis was consistent with the more recent gene flow between the ‘transient’ and ‘offshore’ ecotypes, as also inferred by Hoelzel *et al.* (2007).

From H&M (2016):

*“In their consensus tree, they find a similar topology to our tree (suggesting that alternative filtering did not affect the broader inference)”*

and

*“Further, neither our nuclear tree nor the consensus phylogeny generated in Foote and Morin (2016) support the same topology or inference as the mtDNA tree”*



**Figure 1** Schematic diagrams of the topology of (a) the consensus tree from our multilocus phylogenetic analyses (Foote and Morin, 2016); (b) the nuDNA tree; and (c) mtDNA tree from Moura *et al.* (2015). Each represents the tree-like relationship among the following five populations: Marion Island (M), North Atlantic (A), North Pacific Transient (T), North Pacific Resident (R) and North Pacific Offshore (O). The positions of two taxa interchange between topologies (a, b), and between topologies (b, c).

The positions of two taxa change between the consensus nuDNA tree from Foote and Morin (2016) and the nuDNA tree from Moura *et al.* (2015). Similarly, the positions of two taxa change between the nuDNA tree and the mtDNA tree from Moura *et al.* (2015), see Figure 1. Therefore, H&M's assertion that the two nuclear topologies are 'similar', while neither nuclear tree supports the mtDNA topology, is subjective.

The uncertainty in the relationship among these three interchanging taxa is highlighted in Foote and Morin (2016), and is attributed to incomplete lineage sorting and ancestral admixture. Arguably, there is no 'correct' topology; rather different loci retain a signature of different demographic and evolutionary processes (admixture, shared ancestry, bottlenecks, and so on). We therefore continue to contend that the inference of ancestral geographic distribution based on the branching order of a single sparsely sampled and unresolved topology (that is, Moura *et al.*, 2015) does not capture the true complexity of the evolutionary history of North Pacific killer whale ecotypes.

#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

AD Foote<sup>1</sup> and PA Morin<sup>2</sup>

<sup>1</sup>*Molecular Ecology Fisheries Genetics Lab, School of Biological Sciences, Bangor University, Bangor, Wales, UK and*

<sup>2</sup>*Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, La Jolla, CA, USA*  
E-mail: FooteAD@gmail.com

---

Foote AD, Morin PA (2015). Sympatric speciation in killer whales? *Heredity* **114**: 537–538.

Foote AD, Morin PA (2016). Genome-wide SNP data suggest complex ancestry of sympatric North Pacific killer whale ecotypes. *Heredity* **117**: 316–325.

Hoelzel AR, Hey J, Dahlheim ME, Nicholson C, Burkanov V, Black N (2007). Evolution of population structure in a highly social top predator, the Killer Whale. *Mol Biol Evol* **24**: 1407–1415.

Hoelzel AR, Moura AE (2015). Resource specialisation and the divergence of killer whale populations. *Heredity* **115**: 93–95.

Hoelzel AR, Moura AE (2016). Killer whales differentiating in geographic sympatry facilitated by divergent behavioural traditions. *Heredity* **117**: 481–482.

Moura AE, Kenny JG, Chaudhuri R, Hughes MA, Reisinger RR, de Bruyn PJN *et al.* (2015). Phylogenomics of the killer whale indicates ecotype divergence in sympatry. *Heredity* **114**: 48–55.