

Split Band-rumped Storm-Petrel *Hydrobates castro* into three species**Background:**

The Band-rumped Storm-Petrel complex (*Hydrobates castro sensu lato*) contains seven named taxa distributed across the Atlantic and Pacific Ocean basins. The complex has long been thought to contain multiple cryptic species due to vocal differences between populations and the presence of both hot-season and cool-season breeding populations present on single islands or archipelagos. However, plumage patterns and morphometrics in the group are highly conserved, making it extremely difficult to assign individuals to taxa under field conditions, especially away from breeding colonies.

The named taxa in the group, in order of date of description, are:

castro (Harcourt, 1851) – widespread North Atlantic breeder
jabejabe (Bocage, 1875) – Cape Verde Islands
cryptoleucura (Ridgway, 1882) – Hawaii
bangsi (Nichols, 1914) – Galapagos Islands
helena (Mathews, 1934) – southern Atlantic islands
kumagai (Mathews, 1938) – Japan
monteiroi (Bolton et al., 2008) – Azores hot season breeders

Additionally, at least two breeding populations lack formal taxonomic descriptions. The first consists of North Atlantic cool-season breeders (Howell 2012, Taylor et al. 2019) sometimes called “Grant’s” Storm-Petrel (hot-season North Atlantic breeders are nominate *H. castro*). The second is a population breeding on islands in the Gulf of Guinea (Flood et al. 2012).

The NACC tackled this problem as recently as 2019 in proposal 2019-C-10, which resulted in the unanimous acceptance by the committee of the split of Monteiro’s Storm-Petrel, *H. monteiroi*, from all other taxa in the group. This split was based on the findings of Bolton et al. (2008), who showed convincingly that populations of *monteiroi* and *castro* breeding on the Azores segregated temporally, did not recognize one another vocally, and exhibited very low levels of gene flow, thus qualifying as distinct species under the Biological Species Concept. *Hydrobates monteiroi* has also been recognized by global lists (Clements et al. 2019, HBW and BirdLife International 2019, Gill et al. 2020). Additionally, the population breeding on the Cape Verde Islands has been recognized as a species by several authorities (Clements et al. 2019, HBW and BirdLife International 2019, Gill et al. 2020) under the name Cape Verde Storm-Petrel, *H. jabejabe*, but this split has not yet been considered by the NACC.

A series of publications has tackled the phylogeography of the complex using mitochondrial DNA, microsatellite markers, and small numbers of nuclear loci (Friesen et al. 2007, Sangster et al. 2012, Silva et al. 2016, Smith et al. 2007, Smith and Friesen 2007, Wallace et al. 2017), but each has had either a narrow geographic focus or has lacked genetic samples from some populations or named taxa. Additionally, the complex has been the focus of vocal playback studies (Bolton 2007), which are described in detail below.

As an aside, another recent proposal accepted by the committee (2019-B-7) transferred all species in the genus *Oceanodroma* to *Hydrobates*, due to paraphyly in the former genus (Wallace et al. 2017; *Hydrobates* has priority and is embedded within *Oceanodroma*). The

decision to lump the genera in place of splitting *Oceanodroma* was made in part due to the fact that no name was thought to be available for one of the clades in *Oceanodroma*. That clade contained samples of *monteiroi* and *jabejabe* (= the old *castro*), for which a name is in fact available: *Thalobates* (Mathews 1943), which has *castro* as the type species (Mathews and Hallstrom 1943). Although the current proposal contains insufficient information with which to revisit the generic-level classification of the Hydrobatidae, this is simply to note that should *Hydrobates* be split in the future, the *H. castro* complex could be transferred to *Thalobates*.

New Information:

Taylor et al. (2019) provided, for the first time, a phylogenetic study of Band-rumped Storm-Petrels that included all named populations, both hot- and cool-season breeders, and many thousands of nuclear loci, all of which allows for a more complete revision of the taxonomy of the group. The only unsampled population consists of the as-yet unnamed breeders on islands of the Gulf of Guinea. Taylor et al. (2019) sequenced 3,707 nuclear loci using ddRAD-Seq and two mitochondrial loci (cytochrome *b* and the control region). They estimated phylogenies from the nuclear SNPs using RAxML and SNAPP, and from the mitochondrial data in BEAST.

In both the nuclear and mitochondrial phylogenies, they recovered *monteiroi* as embedded within the currently defined *H. castro* (Figs. 5-7). These phylogenies found with high support that *jabejabe* was sister to the remainder of the group. The topology of the rest of the tree was rather less resolved, with different analyses placing *monteiroi* either as sister to the remaining five taxa (nuclear RAxML tree) or as sister to *castro sensu stricto* (nuclear SNAPP tree, mitochondrial tree).

Two methodological shortfalls are worth mentioning, both of which may affect the taxonomic conclusions. The first is the selection of an outgroup taxon and the second is the model used for the estimation of the RAxML phylogeny. None of the phylogenies estimated by Taylor et al. (2019) used a sample outside of the Band-rumped Storm-Petrel complex as an outgroup. Instead, they opted to root all of the trees with their samples of *jabejabe*, a decision that was based on the mitochondrial cytochrome *b* phylogeny in Wallace et al. (2017), who found *jabejabe* to be sister to the rest of *castro (sensu lato)* and did use an outgroup. Although rooting the mitochondrial phylogeny with *jabejabe* in Taylor et al. (2019) is likely a safe assumption given the similar locus-sampling of the two studies, it is certainly not the case for the tree based on the nuclear SNPs, given the many documented cases of topological discordance between mitochondrial and nuclear phylogenies across the tree of life. Different analyses of the nuclear data in Taylor et al. (2019) show conflicting results with regard to the genetic distinctiveness of each taxon, which would have been clarified by the use of an outgroup. Both the STRUCTURE and PCA results of nuclear SNPs in Taylor et al. (2019) show that *castro (sensu stricto)* is the most genetically distinct taxon analyzed (Figure S3, Figure 3), and *jabejabe* doesn't show up as genetically distinct from the rest of the group in the STRUCTURE results until K=4 (Figure S3A). While PCA and STRUCTURE analyses do not implicitly test phylogenetic relationships, this does suggest that the nuclear and mitochondrial genetic patterns differ, and that rooting the nuclear phylogeny with *jabejabe* is not a safe assumption. However, the SNAPP phylogeny of nuclear data (which does not require the setting of an outgroup) did recover *jabejabe* as sister to the rest of complex. The second factor is the model used to infer the RAxML phylogeny. RAxML provides a SNP-specific model that corrects for the ascertainment bias of using DNA datasets that contain variable sites only, but this appears to have not been used. This, plus the amount of missing data in SNP datasets, has been shown to affect both topology and branch lengths of SNP-based phylogenies (Leaché et al. 2015) and

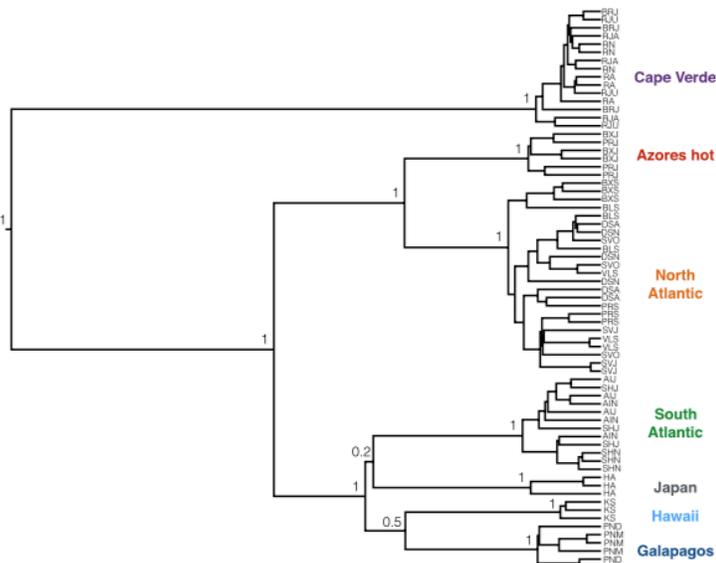


Fig. 5. Bayesian phylogenetic reconstruction of concatenated cytochrome b and control region mitochondrial DNA sequences of the band-rumped storm-petrel species complex, generated in BEAST. Posterior probability values are given above nodes to show support for the seven groups uncovered in our analyses.

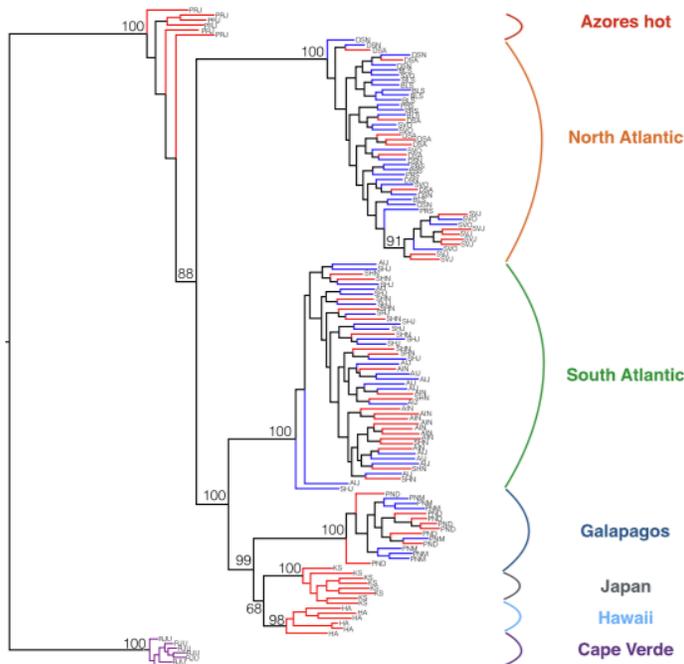


Fig. 6. Maximum likelihood phylogenetic reconstruction of relationships among the band-rumped storm-petrels generated in RAxML. Bootstrap support is given for all nodes with a value above 50. Branches are coloured by the breeding time of the individual bird: red for a bird sampled during the hot season, blue for a bird sampled during the cool season, and purple for a bird sampled from a colony with year-round breeding. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Figures 5, 6 (both above), and 7 (on next page) from Taylor et al., presenting phylogenetic results from Bayesian, maximum likelihood, and SNAPP analyses. For ease of interpretation, I provide here the taxonomic names that correspond to their sampling populations: “North Atlantic” = *castro*, “Azores hot” = *monteiroi*, “South Atlantic” = *helena*, “Cape Verde” = *jabejabe*, “Galapagos” = *bangsi*, “Hawaii” = *cryptoleucura*, “Japan” = *kumagai*.

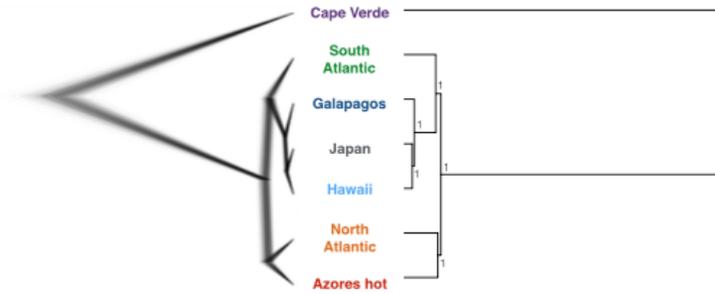
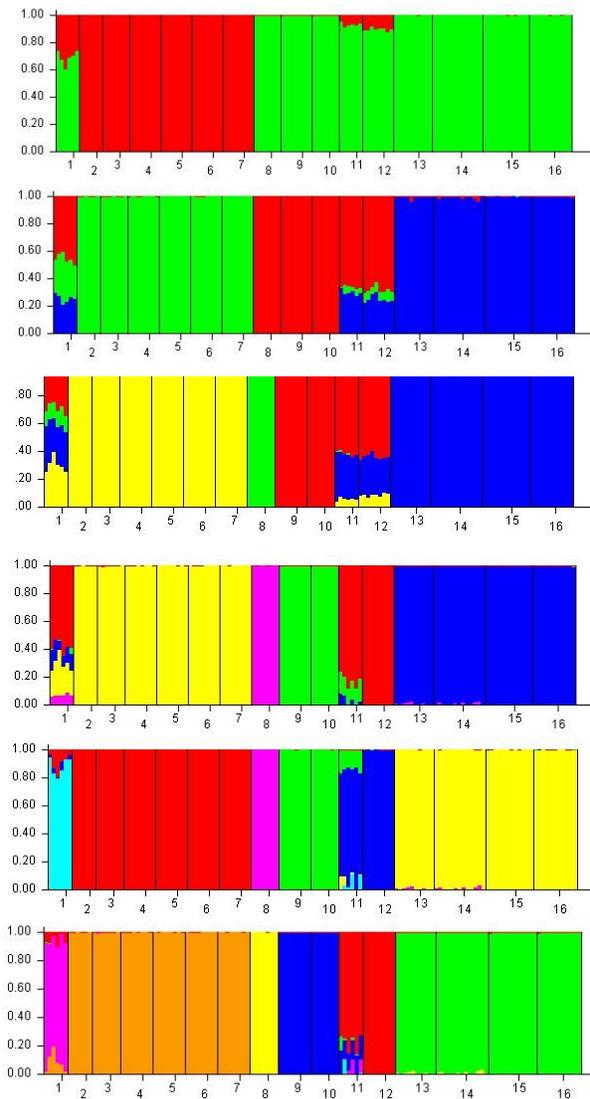


Fig. 7. Phylogenomic reconstruction of the seven genetic groups of band-rumped storm-petrels generated in the SNAPP package in BEAST. The left-hand side shows the denstree and the right-hand side shows the consensus tree with posterior probabilities labelled on the nodes.



Figures S3A and S3B from Taylor et al. (2019). The STRUCTURE results presented in the main paper show all populations for only $K=2$ (the K value with the lowest log likelihood), while $K = 2$ through $K = 7$ are presented only in the supplemental material pasted here. Population assignments: 1 = *monteiroi*, 2-7 = *castro*, 8 = *jabejabe*, 9-10 = *bangsi*, 11 = *cryptoleucura*, 12 = *kumagai*, 13-16 = *helena*.

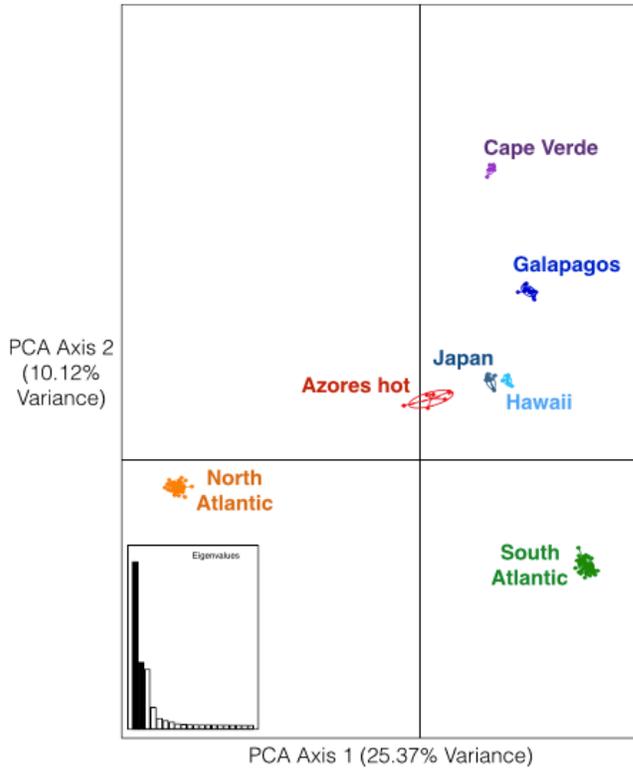


Fig. 3. Results of a principal component analysis of the band-rumped storm-petrel species complex seven genetic groups. Ellipses and colours have been chosen to label the six resultant non-overlapping clusters.

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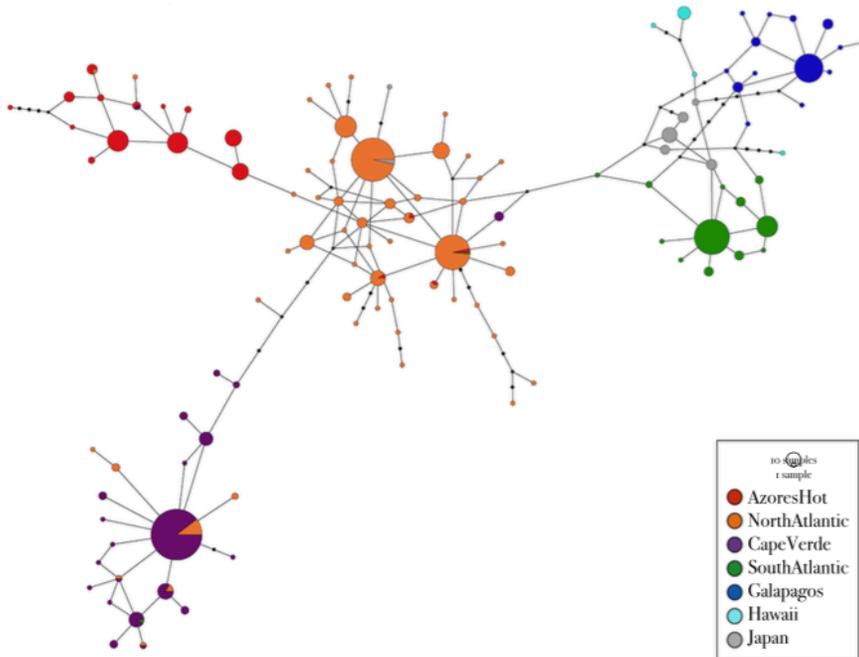


Fig. 4. Statistical parsimony network of 333 bp of the mitochondrial control region of 754 band-rumped storm-petrels. Circle size relates to the number of samples with each haplotype. Black circles represent unsampled or now-extinct haplotypes.

may account for the non-monophyly of *monteiroi* in Figure 6. In fact, using different locus filtering strategies, Taylor et al. (2019) recovered an identical topology to Figure 6, but with all samples of *monteiroi* as monophyletic and in the same position in the tree (Figure S7A, S7B). It is unclear why these phylogenies were presented as supplementary material and not in the main paper. For these reasons, the SNAPP phylogeny should, I think, be given greater weight than the RAxML phylogeny.

The STRUCTURE results show some interesting patterns, with some taxa showing assignments from multiple populations. In particular, all individuals of *monteiroi* show a proportion of genetic assignments from all other populations, perhaps due to either incomplete lineage sorting after a recent divergence or to introgression. Even at K=7 the Japanese and Hawaiian populations do not fully segregate, a finding corroborated by the variable phylogenetic position of *kumagai*. No explicit tests of gene flow were performed, however.

Based on the results of Taylor et al. (2019), the current treatment by the NACC results in a paraphyletic *Hydrobates castro*, although this may be expected given the recent divergence times between taxa in this group (see below), perhaps due to peripatric speciation and rapid evolution of reproductive isolation, at least between some taxa (e.g. *monteiroi*). The three phylogenies presented by Taylor et al. (2019) contain discordant topologies that differ with regard to the position of *monteiroi* and the three Pacific taxa, but a three-way split of *H. castro* would result in monophyletic species according to each phylogenetic hypothesis. Given the strong evidence of reproductive isolation between *monteiroi* and *castro* presented in Bolton et al. (2008) and the unanimous acceptance of *monteiroi* as a species by this committee, the merging of *monteiroi* back into *castro* is not a valid option. A three-way split of *castro* would result in the elevation of *H. jabejabe* (which has been accepted by other global bird checklists) and *H. cryptoleucura* (including *kumagai*, *bangsi*, and *helena*) to species, leaving a monophyletic *H. castro*. Both hot-season and cool-season North Atlantic breeders clustered together in the mitochondrial and RAxML SNP phylogenies, indicating that “Grant’s” Storm-Petrel is not genetically distinct from *castro* and should probably not be treated as a distinct taxon. Clustering the Pacific and South Atlantic taxa under one species makes little biogeographic sense, so an argument could be made to also elevate the South Atlantic taxon *helena* to species level. However, the mitochondrial phylogeny did not recover monophyletic Pacific and South Atlantic groups, but instead recovered *kumagai* as sister to *helena* (to the exclusion of *cryptoleucura* and *bangsi*), albeit with low support. While the two phylogenetic analyses of nuclear data did recover monophyletic Pacific basin or South Atlantic groups, the discordant mitochondrial phylogeny suggests incomplete lineage sorting or introgression between Pacific and South Atlantic populations. The Pacific and South Atlantic populations also cluster together quite closely in the mitochondrial haplotype network (Figure 4).

Based on the reciprocal monophyly of each taxon in all three phylogenies, Taylor et al. (2019) suggested a six-species solution, elevating all taxa to species level with the exception of maintaining *kumagai* as a subspecies of *cryptoleucura* based on the low levels of genetic differentiation between the two taxa in their STRUCTURE analyses. Taylor et al. (2019) did not provide an estimate for the divergence times in the group, but a date is available from Silva et al. (2016) who estimated the divergence of *castro*, *monteiroi*, *kumagai*, and *bangsi* at ~200,000 years using a strict mitochondrial molecular clock. Given how recent the entire radiation is, as well as the lack of explicit tests of introgression between taxa, I think it best to proceed more conservatively for the time being.

Vocal analyses have not been conducted for all taxa, but Bolton (2007) did conduct playback experiments on Azores (*monteiroi*), Galapagos (*bangsi*), and Cape Verde (*jabejabe*) populations

by presenting each of these populations to playback of other taxa (including recordings of *castro*) and control sounds. Some of this evidence was used to support the splitting of *monteiroi* from *castro*. Bolton's results indicate that *monteiroi* and *bangsi* both did not respond to playback of other populations any more than they responded to a control. Cape Verde *jabejabe* did respond more to their own calls than to those of other populations, but showed slightly elevated response to *castro*. Although these data are incomplete for our purposes, they do suggest a pre-zygotic isolation for Pacific Ocean taxa and for *monteiroi*, but are equivocal for *jabejabe*. This is interesting because the some of the phylogenies suggest that *jabejabe* is the most genetically differentiated taxon of the group. It does provide support for species status for *cryptoleucura* (which would include *bangsi*), but additional playback experiments that include *helenae*, *cryptoleucura*, and *kumagai* are desirable. In the Figure 2 from Bolton (2007) shown below, GD=*bangsi*, AH=*monteiroi*, AC=*castro*, CV=*jabejabe*, and CS, SL, and LS are calls from control taxa.

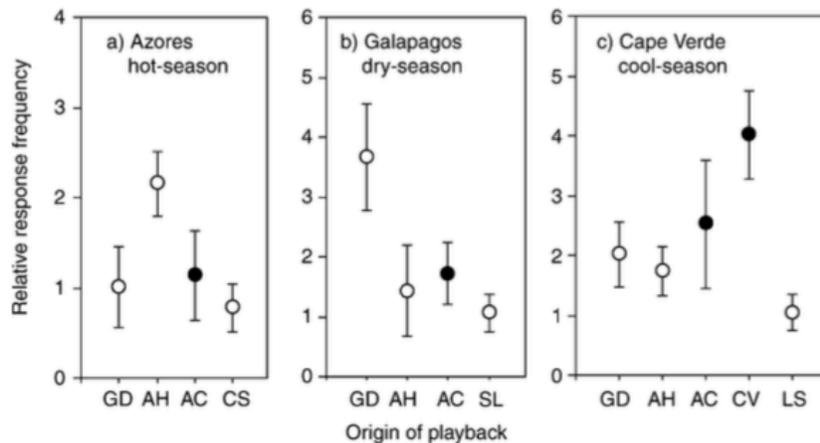


Figure 2. Relative response rate (mean \pm 95% CL) of Madeiran Storm-petrels to playback of Burrow Calls from different populations. (a) Experiment conducted on the Azores hot-season population in June, presenting playback from the Galapagos dry-season (GD), Azores hot-season (AH), Azores cool-season (AC) and Cory's Shearwater (CS) as a control. (b) Experiment conducted on the Galapagos dry-season population in May, presenting playback from the Galapagos dry-season (GD), Azores hot-season (AH), Azores cool-season (AC) and Galapagos Sealions (SL) as a control. (c) Experiment conducted on the Cape Verde cool-season population in December, presenting playback from the Galapagos dry-season (GD), Azores hot-season (AH), Azores cool-season (AC), Cape Verde cool-season (CV) and Little Shearwater (LS) as a control. The relative response rate is the ratio of number of calls during the 5-min playback period to the average number of calls before and after the playback trial (see text for more details). Open symbols = populations nesting May–September, closed symbols = populations nesting October–February. As response rates are calculated relative to background rates, a value of 1 represents the background rate (i.e. in the absence of any playback). Where the confidence limits overlap 1.0, there was no significant increase in Flight Call rate above the background level.

In summary, mitochondrial DNA data support four clusters corresponding to *castro*, *cryptoleucura*, *monteiroi*, and *jabejabe*, but with some shared haplotypes between *castro* and *jabejabe*. The nuclear phylogenies support these same four groups, but may also support *helenae* and *bangsi* as distinct. The SNAPP phylogeny of nuclear data, in particular, supports *jabejabe* as being quite distinct from all other taxa. Branch lengths for all of these groups (except for *jabejabe*) are very short, indicating very recent divergence times for most taxa. The STRUCTURE analysis of nuclear data, however, show extensive shared population assignments (i.e. indicative of introgression or incomplete lineage sorting) in some cases. In particular, *monteiroi* shows shared population assignments from most other taxa (which is of note, considering the documented reproductive isolation from *castro*), and *cryptoleucura/kumagai* show shared population assignments from *bangsi*, *helenae*, and perhaps

to a lesser degree from *castro*. The taxa *castro*, *jabejabe*, *bangsi*, and *helena* showed no (or minimal) shared populations assignments from any other taxa at any value of K. Vocal playback experiments suggest that *monteiroi* and *bangsi* are each distinct (no vocal recognition) from *castro* and *jabejabe*, but are equivocal with regards to *jabejabe* being distinct from *castro*. Vocal playback data are lacking from other taxa.

This is an extremely complex system, and evidence from the mitochondrial DNA, nuclear DNA, and vocal recognition data do not present a clear taxonomic solution. Despite the many studies published on the group thus far, much work remains to be done. Particularly relevant to taxonomic decisions would be studies that include estimates of rates of gene flow between taxa, detailed analyses of song structure, and vocal recognition experiments including all taxa.

Recommendation:

At least four different taxonomic treatments are available given the results from Taylor et al. (2019) and Bolton (2007), and the relative importance given to each line of evidence. Given the arguments outlined above, in particular the nuclear DNA evidence supporting the distinctiveness of *jabejabe* and the vocal data indicating the lack of vocal recognition between *bangsi* and the North Atlantic taxa, **I recommend a four-species treatment for the complex**, which would divide the current *Hydrobates castro* into three species, *H. monteiroi* having already been elevated to species status. This is **option A**:

Hydrobates castro: Widely distributed in the North Atlantic. Contains both hot-season and cool-season breeding populations. The English name Madeiran Storm-Petrel is widely used, although the name is not ideal as the species occurs on other North Atlantic islands.

Hydrobates jabejabe: year-round breeder on the Cape Verde Islands. Known at sea only from the vicinity of the breeding islands. The English name Cape Verde Storm-Petrel is widely used.

Hydrobates cryptoleucura: widely distributed in the Pacific and South Atlantic Oceans, including both hot-season and cool-season breeding populations. Includes the subspecies *bangsi*, *kumagai*, and *helena*. No common name is in wide use for this group. Given that the distribution does not conform to any one biogeographic region and that there are few morphological differences to separate it from other taxa, no clear name is available. If the committee votes to split *cryptoleucura*, I suggest a separate proposal be submitted to address the name for this species, with input from the AOS Committee on Diversity and Inclusion.

Alternatively, given that vocal playback data are not available for some taxa (*helena* in particular), a more conservative treatment would be to hold off on splitting *cryptoleucura* until more vocal data are available. This **three-species treatment** would split *H. jabejabe* from the current *H. castro*. This is **option B**:

Hydrobates castro: Widely distributed in the Atlantic and Pacific basins. Contains both hot-season and cool-season breeding populations of *castro*, and the subspecies *cryptoleucura*, *bangsi*, *kumagai*, and *helena*. The English name Madeiran Storm-Petrel is widely used, although the name is not ideal as the species occurs on many other Atlantic and Pacific islands. In keeping with prior NAOC decisions, I recommend that the name Band-rumped Storm-Petrel be retained for this widespread species, as the splitting of *jabejabe* would elevate a range-restricted taxon from a much more widespread form.

Hydrobates jabejabe: same as in option A.

Two alternative species treatments are available, but I believe that both would need additional evidence from playback experiments, morphological differences, or estimates of gene flow before the splits be considered. I have included them here for the sake of completeness. These treatments are **not recommended**, given the current data available.

1) A five-species treatment, which would be the same as the four-species treatment above, with the additional split of the southern Atlantic *helena* from the three Pacific taxa. Possible English name: Saint Helena Storm-Petrel.

2) A six-species treatment following the recommendation of Taylor et al. (2019), which is the same as 1) with the additional split of the Galapagos taxon *bangsi* from the other two Pacific taxa. Possible English name: Darwin's Storm-Petrel.

Status in the AOU region

Hydrobates jabejabe is known at sea only from the vicinity of the breeding islands, so is best considered extralimital. Both *H. jabejabe* and *H. monteiroi* could occur in the AOU region, but given the difficulty in field identification, either species would likely require DNA sequence data or a band recovery to confirm their occurrence.

Hydrobates castro is thought to be the taxon that occurs regularly as a non-breeding visitor off the east coast of North America and in the Gulf of Mexico. This is supported by a specimen recovered in Alabama that had been banded as a breeding adult in the Azores in September, so is referable to *castro* (Woolfenden et al. 2001).

Hydrobates cryptoleucura breeds in Hawaii. A single record from California (Singer et al. 2020) certainly pertains to one of the Pacific breeding taxa and is thus referable to *H. cryptoleucura* but remains unidentified to subspecies. The South Atlantic taxon *helena* is widespread at sea in the South Atlantic but lacks documented records for our area and is unlikely to occur.

Effect on the AOS Checklist:

Option A would add one species to the AOS Checklist; *H. cryptoleucura*. Option B would add no species to the AOS Checklist.

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Submitted by: Oscar Johnson, Louisiana State University Museum of Natural Science

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