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A phylogenetic test of sympatric speciation in the Hydrobatinae (Aves: Procellariiformes)

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ABSTRACT

Phylogenetic relationships among species can provide insight into how new species arise. For example, careful consideration of both the phylogenetic and geographic distributions of species in a group can reveal the geographic models of speciation within the group. One such model, sympatric speciation, may be more common than previously thought. The Hydrobatinae (Aves: Procellariformes) is a diverse subfamily of Northern Hemisphere storm-petrels for which the taxonomy is unclear. Previous studies showed that *Hydrobates* (formally *Oceanodroma*) *castro* breeding in the Azores during the cool season is sister species to *H. monteiroi*, a hot season breeder at the same locations, which suggests sympatric speciation by allochrony. To test whether other species within the subfamily arose via sympatric speciation by allochrony, we sequenced the cytochrome *b* gene and five nuclear introns to estimate a phylogenetic tree using multispecies coalescent methods, and to test whether species breeding in the same geographic area are monophyletic. We found that speciation within the Hydrobatinae appears to have followed several geographic modes of divergence. Sympatric seasonal species in Japan likely did not arise through sympatric speciation, but allochrony may have played a role in the divergence of *H. matsudairae*, a cool season breeder, and *H. monorhis*, a hot season breeder. No other potential cases of sympatric speciation were discovered within the subfamily. Despite breeding in the same geographic area, hydrobatine storm-petrels breeding in Baja California (*H. microsoma* and *H. melania*) are each sister to a species breeding off the coast of Peru (*H. tethys* and *H. markhami*, respectively). In fact, antitropical sister species appear to have diverged at multiple times, suggesting allochronic divergence might be common. In addition, allopatry has likely played a role in divergence of *H. furcata*, a north Pacific breeder, and *H. pelagius*, a north Atlantic breeder. This study demonstrates that a variety of mechanisms of divergence have played a role in generating the diversity of the Hydrobatinae and supports the current taxonomy of the subfamily.

1. Introduction

Understanding the phylogenetic relationships among species can give insight into how lineages diverged and how new species arise. The process of speciation can be organized based on the geographic overlap of incipient species during divergence. These models of speciation range from complete geographic isolation of incipient species (allopatric speciation) to complete geographic overlap of incipient species (sympatric speciation) with various degrees of geographic overlap in between (peripatric and parapatric speciation; Coyne and Orr, 2004; Fitzpatrick et al., 2009). Although the importance of sympatric speciation as a mode of species generation has been controversial, recent evidence suggests that it may be more common than previously thought. For example, sympatric speciation appears to have been involved in the origin of cichlid species (e.g. *Pundamilia nyererei* and *P. pundamilia*; Seehausen and van Alphen, 1999), palm trees (*Howea belmoreana* and *H. forsteriana*; Gavrilets and Vose, 2007), subterranean blind mole rats (*Spalax galili*; Hadid et al., 2013), and apple maggots (*Rhagoletis pomonella*; Smith, 1988). Sympatric speciation by ecological segregation has also arguably occurred in birds, including *Nesospiza* buntings in the Tristan de Cunha archipelago (Ryan et al., 2007) and Galápagos warbler finches *Certhidea olivacea* and *C. fusca* (Tonnis et al., 2005). Sympatric speciation can also occur by allochrony, where individuals that breed at different

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times are less likely to encounter each other leading to reduced gene flow (Hendry and Day, 2005). For example, in sympatric periodic cicadas (*Magicicada* species), one population emerges on a 13-year cycle whereas another population emerges on a 17-year cycle, resulting in assortative mating and population divergence (Sota et al., 2013). Allochronic speciation can also occur as a result of populations breeding in different seasons, as in summer and winter populations of the pine processionary moth (*Thaumetopoea pityocampa*; Santos et al., 2011).

The Hydrobatinae (Aves: Procellariiformes; Genus: *Hydrobates*, Carboneras and Bonan, 2014; formerly genera *Oceanodroma, Halocyptena*) is a diverse subfamily of mostly Northern Hemisphere seabirds that includes several examples of genetic divergence of sympatric allochronic populations (Table 1). Both the band-rumped storm-petrel *Hydrobates castro* spp. (Monteiro and Furness, 1998; Snow and Snow, 1966) and Leach's storm-petrel (*H. leucorhoa*; Power and Ainley, 1986) have populations that nest in different seasons (hot and cool) on the same island, often using the same burrows. Results from past and ongoing population genetic studies suggest that these seasonal populations originated sympatrically by allochrony (Friesen et al., 2007a; M.F. Silva et al., 2016; Taylor et al., unpubl.). Among other results, this led to distinction of the hot-season breeders from the Azores archipelago as a cryptic species, Monteiro's storm-petrel (*H. monteiroi*; Bolton et al., 2008; Smith et al., 2007). Similarly, previous and on-going studies have found genetic differences between sympatric hot-season and cool-season populations of *H. castro* in the Galápagos (Smith and Friesen, 2007), *H. jabejabe* in Cape Verde (Deane, 2011; Friesen et al., 2007a), and *H. leucorhoa* in Guadalupe (*H. l. cheimomnestes* and *H. l. socorroensis*; Friesen et al., unpubl.).

The Hydrobatinae also include other potential cases of sympatric speciation among the 14 extant and one recently extinct species. Storm-petrels are pelagic, but mostly breed on isolated islands and exhibit high natal philopatry (Brooke, 2004; Warham, 1990). Breeding at their natal site can limit gene flow, likely promoting genetic differentiation between populations (Power and Ainley, 1986). Most species breed in the Northern Atlantic and Pacific oceans, while a few breed in the Southeastern Pacific (Fig. 1). *H. leucorhoa* and *H. castro* are widely distributed in both the Atlantic and Pacific (temperate, and tropical/subtropical, respectively; Brooke, 2004; Warham, 1990) with several defined subspecies and geographic variants (Table 1). Within the *H. castro* complex, in addition to recent recognition of *H. monteiroi* as a good species, *H. jabejabe* (previously classified under *H. castro*) breeding on Cape Verde has been identified as a full species (Sangster et al., 2012; Taylor et al., unpubl.). Within *H. leucorhoa*, four subspecies have been recognized: *H. l. socorroensis*, hot season breeder on Guadalupe I.; *H. l. cheimomnestes*, cool season breeder on Guadalupe I.; *H. l. chapmani*, hot season breeder on islands off Baja California; and *H. l. leucorhoa*, which breeds throughout the North Atlantic and North Pacific oceans (Power and Ainley, 1986). In the North Pacific, the fork-tailed storm-petrel (*H. furcata*) breeds around the Aleutian Islands and the Pacific coast of Canada (Brooke, 2004; Warham, 1990). In the North Atlantic, one subspecies of European storm-petrel (*H. pelagicus pelagicus*) breeds in the Atlantic and the other subspecies (*H. p. melitensis*) breeds in the Mediterranean (Cagnon et al., 2004; Sangster et al., 2012).

Storm-petrels appear to have a few major hotspots of diversity (Fig. 1). For instance, many storm-petrel species breed in the waters around Baja California, Mexico including the least storm-petrel (*H. microsoma)*, black storm-petrel (*H. melania)*, ashy storm-petrel (*H. homochroa)*, three subspecies of *H. leucorhoa*, and the recently extinct *H. macrodactyla* (Brooke, 2004; Warham, 1990). A diversity hotspot also occurs off the coast of Peru, where Markham's storm-petrel (*H. markhami*), and one wedge-rumped storm-petrel subspecies (*H. tethys kelsalli*) breed (Brooke, 2004; Warham, 1990). The other wedge-rumped storm-petrel subspecies (*H. tethys tethys*) breeds around the Galápagos (Brooke, 2004; Warham, 1990). The breeding range of Hornby's storm-petrel (*H. hornbyi*) is unknown as nests have not been found; however observations of it in the waters around Chile and Peru, and observations of fledglings inland, suggest that it nests in this area (Brooke, 1999).

Another hotspot of diversity occurs in the Northwestern Pacific around Japan where Matsudaira's storm-petrel (*H. matsudairae*), Swinhoe's storm-petrel (*H. monorhis*), Tristram's storm-petrel (*H. tristrami*), *H. leucorhoa*, and *H. castro* breed (Brooke, 2004; Warham, 1990). Similar to *H. castro* on the Azores archipelago, these species breed in different seasons in the same geographic area (Brooke, 2004). *H. tristrami* breeds in the cool season from October to June on northwestern Hawaiian Is. and on islands in the Ogasawara Archipelago of Japan (McClelland et al., 2008). *H. matsudairae* also breeds in the cool season but has a breeding range restricted to Iwo Island (Chiba et al., 2007). Historically, *H. matsudairae* and *H. tristrami* bred sympatrically on Iwo I., but their current breeding sites do not overlap (Chiba et al., 2007; Ornithological Society of Japan, 2012). *H. monorhis* breeds in the hot season from June to October (Brooke, 2004) on islands off of Japan, Korea, far east Russia, and China, with its largest breeding colony on Kutsujima I. in the Sea of Japan (Ornithological Society of Japan, 2012; Sato et al., 2010). Currently, *H. tristrami* and *H. monorhis* breed sympatrically at two breeding sites (Hachijo-Kojima I. and Kozushima I.) but in different seasons (McClelland et al., 2008; Ornithological Society of Japan, 2012; Sato et al., 2010). The difference in breeding times between these species in the same geographic area suggests they may have arisen through sympatric speciation by allochrony.

Despite these interesting geographic distributions, the phylogenetic relationships among the species are not well characterized, with only a few partial phylogenies (e.g. Friesen et al., 2007a,b; M.C. Silva et al., 2016; Nunn and Stanley, 1998; Penhallurick and Wink, 2004). For the present study, we used gene trees and a multispecies coalescent model (*Beast; Degnan and Rosenberg, 2009; Heled and Drummond, 2010) based on one mitochondrial segment and five nuclear introns to estimate phylogenetic relationships among all extant species and subspecies (Table 1). Specifically, given previous evidence for sympatric speciation by allochrony (above), we used a phylogenetic approach to test whether the sympatric species with non-overlapping breeding seasons in Japan (*H. tristrami* in the cool season and *H. monorhis* in the hot season) may have arisen through sympatric speciation by allochrony. In addition, we tested whether species breeding in the same geographical area (e.g. Peru, Baja California area) are monophyletic as predicted under sympatric speciation.

2. Materials and methods

2.1. Sample collection and DNA extraction

Tissue, feather or blood samples were obtained for representatives of all extant species of the storm-petrel subfamily Hydrobatinae (Table 1). At least two individuals per species were included in our analysis. Whenever possible, two individuals from each named subspecies or previously identified genetically differentiated conspecific population were also included (e.g. Cagnon et al., 2004; Smith et al., 2007). We also attempted to extract DNA from museum specimens of *H. macrodactyla*; however, these resulted in very poor quality DNA and so this species was not included in the study. Previous studies showed that Hydrobatinae is a monophyletic group, sister to the Oceanitinae (Burleigh et al., 2015; Nunn and Stanley, 1998; Warham, 1990); one Wilson's storm-petrel (*Oceanites oceanicus*) was therefore used as an outgroup.