**Running head: *Hybridisation in albatrosses***

**Breeding-site vagrancy and hybridization in albatrosses**

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Given the rarity of hybridization in seabirds, which presumably relates to their very high philopatry, the degree of breeding-site vagrancy should correspond with the incidence of mixed-species pairing, although not necessarily of hybrids if there are behavioural or genetic barriers to successful reproduction. Using molecular methods, we verified that two of the three chicks hatched by a vagrant male White-capped Albatross *Thalassarche steadi* paired with a female Black-browed Albatross *T. melanophris* at South Georgia were genuine hybrids (these chicks died before fledging, but a third chick – the result of an extra-pair copulation – fledged successfully). In a wider review, we could find only five known or suspected mixed-species pairs, and three different hybrids in albatrosses, mostly between closely-related species. This appears to reflect behavioural barriers to hybridization in sympatric species and the low incidence of breeding-site vagrancy (which mainly involves single individuals that invariably associate with the most phenotypically-similar local taxon). Breeding-site vagrancy is most frequent in the ‘shy-albatross’ complex, which could explain why genetic divergence occurred more recently in this group than in other *Thalassarche*, and hence exploratory behaviour appears to be more important than numerical abundance or breeding distribution in driving colonisation as well as hybridization processes in albatrosses.

**Keywords**: heterospecific pairs, hybrids, inter-breeding, mixed-species pairs, range expansion, secondary contact

Hybridization is common phenomenon in birds, particularly between closely-related species breeding in sympatry, but is relatively rare in seabirds compared with terrestrial birds ([Grant & Grant 1992](#_ENREF_20)). Indeed, heterospecific (mixed-species) pairings, assumed or verified hybrids (adults or juveniles) are only recorded between 25 different species-pairs in seabirds, particularly in the Charadriiformes (guillemots, gulls, terns and skuas) ([reviewed by Brown *et al.* 2015](#_ENREF_6)). The low overall incidence of hybridisation may reflect their typically high philopatry. If so, we might expect the degree of breeding-site vagrancy to correspond with the incidence of mixed-species pairing, although not necessarily of hybrids if there are behavioural or genetic barriers to successful reproduction. Hybridisation is important from an evolutionary perspective; where pre- and post-mating barriers are weak, hybridization following secondary contact is more likely and can affect genetic structure. This has occurred at Campbell Island (New Zealand) where Black-browed Albatrosses *Thalassarche melanophris* from multiple lineages have probably colonised only in the last 50 years ([Moore *et al.* 2001](#_ENREF_24), [Burg *et al.* 2017](#_ENREF_7)), and at Round Island (near Mauritius), where three species of gadfly petrels *Pterodroma* spp. established in the last century, and readily hybridise ([Brown *et al.* 2011](#_ENREF_5)).

Although infrequent, hybridization is recorded in 10 species-pairs of Procellariiformes (albatrosses, petrels and shearwaters), usually involving secondary contact between taxa that are closely related and previously considered to be subspecies ([Moore *et al.* 1997](#_ENREF_25), [Curé *et al.* 2010](#_ENREF_17), [Brown *et al.* 2011](#_ENREF_5), [Brown *et al.* 2015](#_ENREF_6)). The exceptions include hybrids between Laysan Albatross *Phoebastria immutabilis* and Black-footed Albatross *P. nigripes*, which are distinct species; these were first noted in the late 1800s on islands in northwest Hawaii where the two species breed in sympatry in very large numbers (1000s of pairs) ([Fisher 1972](#_ENREF_18)). Hybridization involving an immigrant at the breeding site of a previously allopatric procellariform species is even less frequent ([Brown *et al.* 2015](#_ENREF_6)). This is probably because although at-sea ranges are extensive in this order, natal philopatry is very strong (Warham 1990). In addition, heterospecific pairings are thought to be limited in Procellariiformes by behavioural barriers such as differences in vocalisations or displays (Warham 1996), and in seabirds in general by differences in bill and foot colouration ([Pierotti 1987](#_ENREF_29)). Breeding success is usually lower in mixed-species than conspecific pairs, and hybrids may have difficulties in securing partners when they try to recruit (Brown et al. 2015; Warham 1990). Back-crossing is therefore extremely rare unless the parental species were closely-related; however, exceptions include hybrids between Northern Royal Albatross *Diomedea sanfordi* xSouthern Royal Albatross *D. epomophora*, formerly considered to be subspecies, which breed with Northern Royal Albatrosses at Taiaroa Head (Agreement on the Conservation of Albatrosses and Petrels 2009). In contrast, at Laysan Island (Hawaii), only one of five F1 hybrid Laysan x Black-footed Albatrosses observed in 2011 bred with a Laysan Albatross; however, there were several putative F2 backcrosses ([Rutt 2013](#_ENREF_34)), and an F1 hybrid with a Laysan Albatross partner has successfully raised chicks on Midway since 2006 ([Rohwer *et al.* 2014](#_ENREF_33)).

Hybridization in nature is predominantly unidirectional ([Wirtz 1999](#_ENREF_43)). This also applies to the albatrosses; hybridization has only been verified between male Black-footed Albatrosses which force extra-pair copulations on female Laysan Albatrosses ([Rohwer *et al.* 2014](#_ENREF_33)), male Northern Royal and female Southern Royal Albatrosses ([Robertson 1993](#_ENREF_32)), and, predominantly, male Black-browed Albatrosses *Thalassarche melanophris* and female Campbell Albatrosses *T. impavida* ([Moore *et al.* 2001](#_ENREF_24)). Here using molecular methods we verify hybrid chicks resulting from the pairing of a male White-capped Albatross *Thalassarche steadi* and a female Black-browed Albatross at South Georgia. Although White-capped Albatross is considered by some authorities to be a subspecies of Shy Albatross *T. cauta*, for the sake of taxonomic stability we consider them to be separate species following the recommendations of the Taxonomy Working Group of the Agreement on the Conservation of Albatrosses and Petrels (ACAP), and of BirdLife International (Phillips et al. 2016).We also review incidences of hybridization and breeding-site vagrancy in albatrosses and discuss the results in the context of ecological explanations and evolutionary implications.

**METHODS**

The White-capped Albatross is endemic to New Zealand. The vast majority breed at the Auckland Islands and feed in New Zealand waters, although the at-sea distribution expands in the non-breeding season to include southeast Australia, and juveniles and some adults use southern African and occasionally South American waters ([Tickell 2000](#_ENREF_39)). A male White-capped Albatross was first observed at Bird Island, South Georgia (54°00'S, 38°03'W) in a sub-colony of c. 1000 pairs of Black-browed Albatrosses on 7 February, 2003; the bird was blood-sampled, and sex and species determined using molecular methods ([Phalan *et al.* 2005](#_ENREF_27)). The sub-colony was visited two or three times in incubation and chick-rearing in subsequent seasons to record breeding activities and take tissue samples (blood or feathers) from the chicks. Albatrosses lay a single egg per breeding attempt and there is no replacement.

DNA was extracted from blood or feathers from the putative hybrid chicks using a modified Chelex extraction ([Walsh *et al.* 1991](#_ENREF_41), [Burg & Croxall 2001](#_ENREF_8))*.* Reference samples from three Black-browed Albatrosses at South Georgia, and six White-capped Albatrosses bycaught in fisheries off South Africa were sequenced to assess genetic differences between the two parental species. Samples were sequenced at four loci, including a single mitochondrial locus (mtDNA, control region) and three nuclear loci (Pema7, Pema 13 and Occa9). MtDNA was amplified in a 25 µl reaction containing 200 µM dNTP, 2.5 mM MgCl2, 2 µM of each specF1 and GluR7 ([Abbott & Double 2003b](#_ENREF_2)) primer, and 0.5 U taq. The thermal profile consisted of 94°C for 2 minutes followed by two cycles at 94°C for 25 s, TaTD for 25 s, and 72°C for 25 s; 30 cycles at 94°C for 25 s, 50°C for 25 s and 72°C for 25 s; and a final cycle of 72°C for 2 minutes. For the initial touchdown cycles (TaTD), the annealing temperature started at 65°C and decreased to 60°C and 55°C for each subsequent pair. Pema 7 and Pema 13 ([Silva *et al.* 2011](#_ENREF_36)) were amplified using the same PCR profile: one cycle at 94°C for 2 min, 54°C for 45 s, 72°C for 1 min; 37 cycles at 94°C for 30 s, 54°C for 45 s, 72°C for 1 min; and one cycle of 72°C for 5 min. PCR reactions were similar to those for mtDNA, with the exception of 1 mM MgCl2 for Pema 7 and 1.5 mM MgCl2 for Pema13. The Occa9 ([Silva *et al.* 2012](#_ENREF_37))locus was amplified using the same PCR profile and reaction conditions as Pema13 but with a 60°C annealing temperature. All samples were sent to Genome Quebec for sequencing. Chromatograms were checked and aligned using MEGA4 ([Tamura *et al.* 2007](#_ENREF_38)). Samples from the three putative hybrid chicks were compared to the reference sequences.

**RESULTS**

The White-capped Albatross was first recorded in 2002/03, and seen on several occasions but did not breed in 2003/04, 2004/05, 2005/06 or 2006/07. It bred with an un-ringed Black-browed Albatross in 2007/08 (five seasons after the first sighting), 2008/09 and 2009/10. All eggs hatched (on 9 or 10 January 2008, 13 January 2009 and unknown date in 2010). All chicks appeared to develop normally, but those hatched in 2008 and 2009 were found dead (on 10 April 2008 and 9 February 2009), and the other chick fledged successfully (on 2-5 May 2010). The White-capped Albatross was not seen in the 2010/11 season although an un-ringed Black-browed Albatross, which may have been its previous partner, incubated an egg on the usual nest (but failed within a week), nor was it observed in subsequent seasons.

Morphologically, the hybrid chicks were indistinguishable from Black-browed Albatross chicks in plumage colouration of the head, body and upper wing region. The culmen (dorsal side of the upper mandible) of the hybrid chicks appeared to be wider than that of a Black-browed Albatross, but no measurements were available from the fully-grown chick for this to be verified.

The 338 bp mtDNA sequences contained 47 variable sites; 28 of those were fixed differences between Black-browed and White-capped Albatrosses. DNA of the chicks from 2009 and 2010 matched the reference Black-browed Albatross sequences and were identical to each other, indicative of a Black-browed Albatross mother. We were unable to sequence the control region for the chick from 2008. The 665 bp of sequence from Pema13 contained four variable sites and no fixed differences were found between the two species. At position 254, the Black-browed Albatross alleles contained an A (*n* = 1) or G (*n* = 5) whereas all the White-capped alleles (*n* = 10) were A. The chicks from 2009 and 2010 were, respectively, heterozygous (A/G) and homozygous for G. Pema7 contained six variable sites in 696 bp of sequence and only one site (469) was fixed between the two species. At this site, the chicks from 2009 and 2010 were, respectively, heterozygous (A/G) and homozygous for G, the latter matching Black-browed Albatross. The chick from 2008 showed differential amplification of the White-capped Albatross allele (A at position 469). Occa9 was the most variable of the three nuclear loci with 48 of the 695 bp containing variable sites in the reference samples. Of these, only five sites were fixed between the two species: at position 501, all Black-browed Albatrosses had an A and all White-capped Albatross a C, and; at positions 93-96, all Black-browed Albatross had a 4 bp deletion whereas all White-capped Albatross had ‘GGCA’. Multiple sequences from separate PCRs for the chick from 2008 showed alleles of both White-capped and Black-browed Albatrosses. Similarly, the chick from 2009 was heterozygous for White-capped and Black-browed Albatross alleles. As Occa9 was the most variable nuclear locus and DNA from the chick in 2008 showed differential amplification, amplification and sequencing of the sample from the chick in 2010 was carried out four times. All four results were identical, with no evidence of the White-capped Albatross allele.

Based on these data, the chicks from 2009 and 2010 had mtDNA consistent with a Black-browed Albatross mother. The sample from the chick in 2008 only provided nuclear data for two of the three loci; however, those two are the more variable loci and indicate hybrid ancestry. Based on all three nuclear loci, the chick from 2009 was confirmed as a F1 hybrid between White-capped and Black-browed Albatrosses. The genotype of the chick from 2010 was consistent with two Black-browed Albatross parents at all three loci.

**DISCUSSION**

This study confirms the hatching of hybrid chicks in two successive seasons from the pairing of a male White-capped Albatross and female Black-browed Albatross. Genetic analyses indicated that both parents of the third, and last, chick – the only one to fledge successfully - were Black-browed Albatrosses, indicating extra-pair paternity (EPP). EPP in Black-browed Albatrosses at this site is common, accounting for as many as 9% of chicks in some years ([Burg & Croxall 2006](#_ENREF_9)).

In our review, we found reports of five other known or suspected mixed-species pairs in albatrosses, but only three hybrid individuals; Laysan x Black-footed Albatross, Northern x Southern Royal Albatross, Black-browed x Campbell Albatross (Table 1). These species-pairs are considerably closer genetically than Black-browed and White-capped Albatrosses according to the best-fit topology based on available DNA barcodes ([Chambers *et al.* 2009](#_ENREF_10)). Indeed, the two royal albatrosses, and Black-browed and Campbell Albatrosses were considered to be subspecies until recently ([Chambers *et al.* 2009](#_ENREF_10), [Burg *et al.* 2017](#_ENREF_7)).

That heterospecific pairings are so rare (Table 1), even though multiple species of albatrosses breed in sympatry at numerous sites worldwide ([Phillips *et al.* 2016](#_ENREF_28)) tends to confirm the view of Warham ([1996](#_ENREF_42)) that the main barriers to hybridization in the Procellariiformes are behavioural. However, the White-capped Albatross at Bird Island had found a cooperative partner ([probably the same female given the very long pair-bonds typical of albatrosses; Tickell 2000](#_ENREF_39)) indicating that the displays and vocalisations were not so different as to represent barriers to reproduction. Moreover, the interval of five years between first sighting and first breeding was as expected; modal ages for these are five and ten years, respectively, in Black-browed Albatrosses ([Tickell 2000](#_ENREF_39)). Together with observations of heterospecific pairings elsewhere (Table 1) it seems that only the hybridization between Black-footed and Laysan Albatross involves forced extra-pair copulations ([Rohwer *et al.* 2014](#_ENREF_33)). It is therefore important not to generalise from the well-studied situation in Hawaii as to the typical hybridization process in albatrosses, as in all other cases genuine mixed-species partnerships were formed.

A mismatch in timing of reproduction (allochrony) can be a barrier to hybridization. White-capped Albatross chicks do not start hatching at Disappointment Island (Auckland Islands) until 19 January ([Clark & Robertson 1996](#_ENREF_11)), which is after the last hatching date of Black-browed Albatross at South Georgia ([Tickell 2000](#_ENREF_39)). Known hatching dates (9-10 Jan. and 13 Jan.) of the hybrid chicks were relatively late ( < 8% of Black-browed Albatross eggs hatch on or after 9 Jan.; British Antarctic Survey unpubl. data). Similarly, female Northern Giant Petrels *Macronectes halli* paired with male Southern Giant Petrels *M. giganteus* tend to lay later on average than those in conspecific pairs ([Brown *et al.* 2015](#_ENREF_6)). Such results suggest either a limit to how early a male paired with a female of an earlier-laying species can attain breeding condition, or that females in heterospecific pairs are those that tend to lay later than many of their conspecifics.

Although many breeding-site vagrants will go unreported, particularly if very similar in appearance to native species, there are numerous well-monitored albatross colonies world-wide. Given the paucity of records, breeding-site vagrancy appears to be very rare in albatrosses, and mainly involves single individuals far outside their normal breeding range, invariably associating with the local taxon that is phenotypically the most similar (Table 1). It must therefore be rare for multiple vagrants of the same species to establish a new colony at another island group. However, it does occur: single pairs of Antipodean Albatrosses *Diomedea antipodensis* bred for the first time at three different sites in the Chatham Islands in 2003-2005 ([Miskelly *et al.* 2008](#_ENREF_23)), and four pairs of Salvin’s Albatrosses *Thalassarche salvini* were discovered on Penguin Island, Crozet in 1986, including one bird ringed five years earlier and over 6,000 km away when it had visited South Georgia ([Jouventin 1988](#_ENREF_21)).

There are two reports of breeding-site vagrancy involving Black-browed Albatrosses (Table 1), which is perhaps unsurprising as this is by far the most common and one of the most widespread albatrosses in the Southern Ocean ([691,046 pairs and 65 sites; Phillips *et al.* 2016](#_ENREF_28)). Less expected were eight reports involving the ‘shy-albatross’ complex (White-capped Albatross, Shy Albatross, Chatham Albatross *Thalassarche eremita* andSalvin’s Albatross). White-capped Albatross is also relatively common (100,500 pairs), but the global population size of Chatham Albatross (5200 pairs) is very small, and even that of Salvin’s Albatross (41,100 pairs) is considerably smaller than Grey-headed Albatross (98,100 pairs), and not much larger than that of Indian Yellow-nosed, Atlantic Yellow-nosed and Buller’s Albatross ([39,319 pairs, 33,650 pairs, 30,069 pairs, respectively; Phillips *et al.* 2016](#_ENREF_28)). Albeit with the caveat that some taxa are hard to distinguish (leading to under-reporting), it appears that species in the ‘shy-albatross’ complex are more peripatetic, i.e. more likely to be reported as breeding-site vagrants than other albatross taxa, and therefore more likely to hybridise. It could be no coincidence that the most recent genetic divergence within the *Thalassarche* genus was the separation of Shy Albatross in Tasmania following range expansion of White-capped Albatross ([Abbott & Double 2003a](#_ENREF_1)). There is a suggestion that a ‘dispersal phenotype’ exists in some seabirds ([Kim *et al.* 2007](#_ENREF_22)), and exploratory behaviour may be more of a factor than numerical abundance or breeding distribution in driving colonisation as well as hybridization processes in albatrosses. Finally, it is worth noting that although many albatross populations face major threats at sea, and in some cases on land ([Phillips *et al.* 2016](#_ENREF_28)), rates of hybridization are far lower than would suggest any obvious risk to their conservation. Under such circumstances, management responses appear to be unnecessary ([Genovart 2009](#_ENREF_19)).

**Table 1.** Reported breeding-site vagrancy, mixed-species (heterospecific) pairing and hybrids in albatrosses. V - breeding-site vagrancy (birds in or over-flying colonies of other species). S - sympatric species (at least since the first season indicated). Excludes vagrants at sites where at least one pair of conspecific has bred, or where decoys were used for attraction.

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| --- | --- | --- | --- | --- | --- | --- |
| Rarer species at site | Status | Majority species at site | Site | Breeding seasons | Status | Reference |
| Northern Royal Albatross  *Diomedea sanfordi* | S | Southern Royal Albatross  *Diomedea epomophora* | Taiaroa Head, New Zealand | 1980s-present | Multiple mixed-species pairs with egg or chick; known hybrids breeding | Agreement on the Conservation of Albatrosses and Petrels ([2009](#_ENREF_3)); Robertson ([1993](#_ENREF_32)) |
| Northern Royal Albatross  *Diomedea sanfordi* | V | Southern Royal Albatross  *Diomedea epomophora* | Enderby Island, Auckland Islands | 1992/93-1994/95 | Two mixed-species pairs with egg or chick | Croxall and Gales ([1998](#_ENREF_16)) |
| Antipodean Albatross  *Diomedea antipodensis* | V | Wandering Albatross  *Diomedea exulans* | Bird Island, South Georgia | 2009/10 | Single adult present | British Antarctic Survey unpublished data |
| Black-browed Albatross  *Thalassarche melanophris* | V | Grey-headed Albatross  *Thalassarche chrysostoma* | Marion Island | 2000/01, 2002/03, 2006/07, 2008/09, 2017/18 | Mixed-species pair with egg/chick (1st four years) or single adult present (2017/18) | Ryan *et al.* ([2009](#_ENREF_35)); M. Jones & P.G. Ryan *in litt*. |
| Black-browed Albatross *Thalassarche melanophris* | S | Campbell Albatross  *Thalassarche impavida* | Campbell Island | 1970s-present | Multiple mixed-species pairs with egg or chick; known hybrids breeding | Moore *et al.* ([2001](#_ENREF_24)) |
| Grey-headed Albatross  *Thalassarche chrysostoma* | V | Black-browed Albatross *Thalassarche melanophris* | Falkland Islands | 1952-1956, 1969 (West Point); 2000/01, c.2005, 2010/11 (Beauchêne Island); 2005/06 (Bird Island); 1990s (New Island); 2010 or 2011, 2014/15 (Steeple Jason Island) | Single adults present | Cooper ([2015b](#_ENREF_14)) |
| White-capped Albatross  *Thalassarche steadi* | V | Black-browed Albatross  *Thalassarche melanophris* | Bird Island, South Georgia | 2002/03 to 2009/10 | Single adult present (2002/03 to 20006/07), mixed-species pair with chick (2007/08 to 2009/10) | Phalan *et al.* ([2005](#_ENREF_27)); this study |
| White-capped Albatross  *Thalassarche steadi* | V | Salvin’s Albatross  *Thalassarche salvini* | Western Chain, Snares Islands | 2009/10 | Bird with egg, partner unknown (Rima Islet) | Cooper ([2010](#_ENREF_12)) |
| ‘Shy-type’ albatross  *Thalassarche cauta/steadi* | V | Grey-headed Albatross  *Thalassarche chrysostoma* | Prince Edward Island | 2008/09 | Probable mixed-species pair (egg; partner unknown) | Oosthuizen et al. ([2009](#_ENREF_26)) |
| Salvin’s Albatross  *Thalassarche salvini* | V | Black-browed Albatross  *Thalassarche melanophris* | Bird Island, South Georgia | 1981/82 | Single adult present (also over-flew colony in 1982/83) | Prince and Croxall ([1996](#_ENREF_30)) |
| Salvin’s Albatross  *Thalassarche salvini* | V | Black-browed Albatross  *Thalassarche melanophris* | Cañon des Sourcils Noirs, Kerguelen | 1995/96-1997/98 | Single adult present | Cooper ([2010](#_ENREF_15)) |
| Salvin’s Albatross  *Thalassarche salvini* | V | Black-browed Albatross  *Thalassarche melanophris* | Gonzalo Island, Diego Ramirez, Chile | 2001/02 | Single adult present | Arata ([2003](#_ENREF_4)) |
| Salvin’s Albatross  *Thalassarche salvini* | V | Atlantic Yellow-nosed Albatross  *Thalassarche chlororhynchos* | Gough Island | 2008/09 and 2014/15 | Single adult present | Cooper ([2015a](#_ENREF_13)){, 2010 #3330;Cooper, 2015 #3333}; Visser *et al.* ([2009](#_ENREF_40)) |
| Chatham Albatross  *Thalassarche eremita* | V | Salvin’s Albatross  *Thalassarche salvini* | Western Chain, Snares Islands | 2008/09, 2009/10 | Birds with egg, partners unknown (Rima and Toru Islets 2008/09); mixed-species pair with egg (Toru Islet 2009/10) | Cooper ([2010](#_ENREF_12)) |
| Black-footed Albatross  *Phoebastria nigripes* | S | Laysan Albatross  *Phoebastria immutabilis* | Midway Atoll, Hawaii | 1891-present | Known hybrids breeding (although uncommon; always with Laysan Albatross) | Rohwer *et al.* ([2014](#_ENREF_33)); Rutt ([2013](#_ENREF_34)) |
| Black-footed Albatross  *Phoebastria nigripes* | S | Laysan Albatross  *Phoebastria immutabilis* | Sand and Eastern Islands, Hawaii | 1940s | Putative hybrids | Tickell ([2000](#_ENREF_39)) |
| Salvin’s Albatross  *Thalassarche salvini* | V | Laysan Albatross  *Phoebastria nigripes* | Midway Atoll, Hawaii | 2003 | Single adult present | ([Robertson & Klavitter 2005](#_ENREF_31)) |

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