

Provenance and sex ratio of Black-browed Albatross, *Thalassarche melanophrys*, breeding on Campbell Island, New Zealand

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Abstract. Small numbers of Black-browed Albatross, *Thalassarche melanophrys*, breed on Campbell Island, New Zealand. Their dark brown irises had previously been used to distinguish them from the more numerous Campbell Albatross, *T. impavida*, which has light irises. Blood samples were collected from dark-eyed birds and their partners on Campbell Island to determine their provenance and whether a sex imbalance caused them to breed with Campbell Albatrosses. Analysis of mitochondrial DNA revealed that dark-eyed birds were of three genetically distinct groups: *T. melanophrys*, Falkland Islands *T. melanophrys* and *T. impavida*. The majority of both types of *T. melanophrys* on Campbell Island were male, hence none was paired with the same taxon, but most of the more widespread form chose dark-eyed mates. Other individuals had a succession of light-eyed partners over several years. Dark-eyed *T. impavida* may have been hybrid progeny of female *T. impavida* × male *T. melanophrys* pairings. One of these birds was banded as a chick in 1970, suggesting that hybridisation has occurred on Campbell Island at least as early as that date. Their presence suggests a low rate of interchange between the island groups or recent immigration of *T. melanophrys* to Campbell Island and neighbouring island groups.

Introduction

The Black-browed Albatross, *Diomedea melanophrys melanophrys* (Marchant and Higgins 1990), numbers approximately 680 000 breeding pairs and has a wide distribution throughout the subantarctic islands of the southern oceans (Gales 1998). Its closest relative, the New Zealand Black-browed Albatross, *Diomedea m. impavida*, is found on Campbell Island in the New Zealand subantarctic (Marchant and Higgins 1990; Turbott 1990) and numbers approximately 26 000 pairs (Moore *et al.* 1997).

Recently it was proposed, as part of a taxonomic revision of the albatrosses, that the two subspecies be elevated to species: Black-browed Albatross, *Thalassarche Melanophrys*, and Campbell Albatross, *T. impavida* (Robertson and Nunn 1998). Further genetic work using mitochondrial (mt) DNA and microsatellites confirmed the distinctiveness of *T. impavida* and revealed that *T. melanophrys* from the Falkland Islands differed from those at several other major breeding sites (Diego Ramirez, South Georgia, Kerguelen: Fig. 1). The level of genetic differentiation was higher than that found between other subspecies or species for which comparable studies have been carried out (Burg 2000). Further work is required on the taxonomy of the whole albatross family, especially as new genetic techniques have, in many instances, identified island-specific differences and not all breeding localities have been sampled (Robertson and Nunn

1998). Although not all breeding localities for Black-browed Albatross were sampled (Burg 2000), the current state of knowledge suggests that at least three forms exist, and for the purposes of this paper these will be referred to as *T. melanophrys*, Falkland Islands *T. melanophrys* and *T. impavida*.

The Campbell Albatross is distinguishable from the Black-browed Albatross by having a light yellow or honey-coloured (rather than dark blackish-brown) iris, as well as by some differences in plumage (e.g. heavier black brow) and vocalisations (Marchant and Higgins 1990). The chicks of both species have dark irises, but in Campbell Albatrosses they lighten in colour before adulthood (Marchant and Higgins 1990). Small numbers of Black-browed Albatrosses nest amongst the more numerous Campbell Albatrosses on Campbell Island and the two species interbreed (Moore *et al.* 1997). It was not known whether this was caused by a recent immigration event, and if there was a sex imbalance amongst the rarer immigrants or if resulting hybrid young were recruited into the population (Moore *et al.* 1997). This paper examines these questions using analysis of blood samples for sex and genetic differences.

Methods

Individuals studied, morphometrics and sample collection

All albatrosses studied were from the Campbell Island population (Fig. 1). Dark-eyed birds (Fig. 2a), presumed to be Black-browed Albatross, were searched for amongst the more numerous light-eyed

Campbell Albatross (Fig. 2b) during census of colonies in October 1996; if they were incubating an egg, their nests were marked. Some dark-eyed birds shared characteristics of Campbell Albatross, such as more extensive black brows. Also, a few birds with intermediate eye colour (e.g. mid-brown, smokey or speckled brown) were included in the dark-eyed group. Where possible, the breeding partner was identified during subsequent visits to the colonies in October–November 1996, and blood samples and measurements taken. Blood samples were collected from the tarsal vein of 33 birds and were preserved in Seutin buffer (Seutin *et al.* 1991). The birds sampled comprised: 10 light-eyed birds from five breeding pairs; five light-eyed and seven dark-eyed birds from seven interbreeding pairs; nine dark-eyed birds from five breeding pairs; one dark-eyed bird with an unknown partner; and one dark-eyed non-breeder (i.e. in total, 15 birds with light irises and 18 birds with dark irises). Most birds that were bled were measured for bill dimensions, tarsus and mid toe (Table 1) (Marchant and Higgins 1990; Sagar *et al.* 1998). Some that were nervous or appeared stressed were not measured. In 1999 a further 15 blood samples of light-eyed birds were collected and preserved in 95% ethanol. These birds were not measured.

DNA-based assignment of sex

Birds have two sex chromosomes (Z and W), males being homogametic (ZZ) and females heterogametic (ZW). The sex of albatrosses was determined using a region of the avian chromo-helicase-DNA binding (*CHD*) gene (Griffiths *et al.* 1998; Kahn *et al.* 1998; Fridolfsson and Ellegren 1999). DNA was extracted using a standard phenol/chloroform method (Sambrook *et al.* 1989). Sex-linked variation at the *CHD* locus was assessed using the polymerase chain reaction (PCR) and restriction enzyme digestion. The primers P2 (5'-TCTGCATCGCTAAATCCTTT-3') in combination with either P3 (5'-AGATATTC-CGGATCTGATA-3') or P8 (5'-CTCCCAAGGATGAGRAAYTG-3') (Griffiths *et al.* 1996, 1998) were used. These primer pairs amplify a homologous region on the W and Z chromosome that differs in the pres-

ence or absence of a *Hae* III restriction site. Reactions were performed in a total volume of 25 μ L containing *c.* 50–100 ng of template, 0.6 μ M of each primer, 200 μ M each dNTP, 2 mM $MgCl_2$, 10 mM Tris-HCl pH 8.3, 50 mM KCl and 0.5 units of *Taq* DNA polymerase (*AmpliTaq*, Perkin Elmer). The thermal profile of PCRs was typically 30 s at 94°C (denaturation), 30 s at 45–50°C (annealing) and 30 s at 72°C (extension) for 35–40 cycles. Amplified *CHD* sequences were digested with the restriction enzyme *Hae* III according to the manufacturer's instructions. Digested PCR products were analysed by electrophoresis through a 2% agarose gel (FMC Bioproducts, Seakem/Nusieve 1:1) in 1 \times TBE with 0.5 μ g mL⁻¹ ethidium bromide and visualised under UV light.

Mitochondrial DNA

The 30 blood samples from Campbell Albatrosses and 18 from dark-eyed birds on Campbell Island were included in a larger study of albatross affinities (Burg 2000). In that study 73 blood samples from five islands (Falklands, Diego Ramirez, Bird Island (South Georgia), Kerguelen and Campbell) were sequenced for mtDNA. Three genetically distinct forms were identified (*T. melanophrys*, Falkland Islands *T. melanophrys* and *T. impavida*) and three sets of PCR primers of mtDNA were developed to identify them. Then 115 samples from Falk-

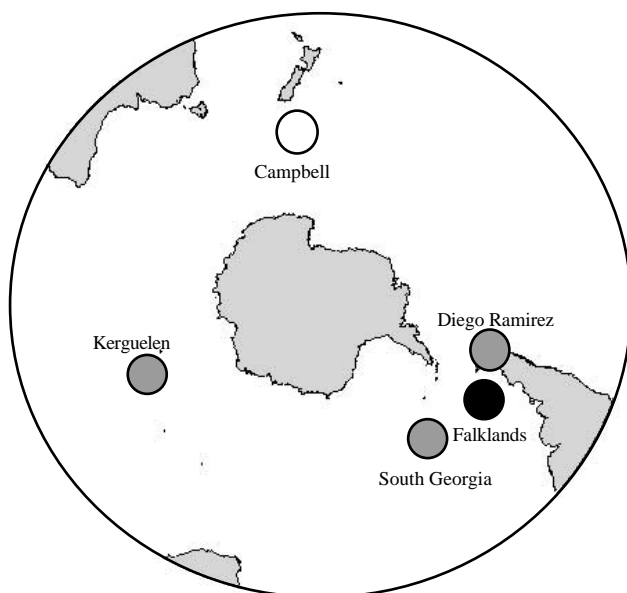


Fig. 1. Map of the southern oceans and landmasses showing the three genetically distinct groups of albatrosses: Campbell Albatross, *T. impavida*, on Campbell Island (white circle); *T. melanophrys* on Diego Ramirez/South Georgia/Kerguelen (dark grey); and Falkland Islands *T. melanophrys* (black).

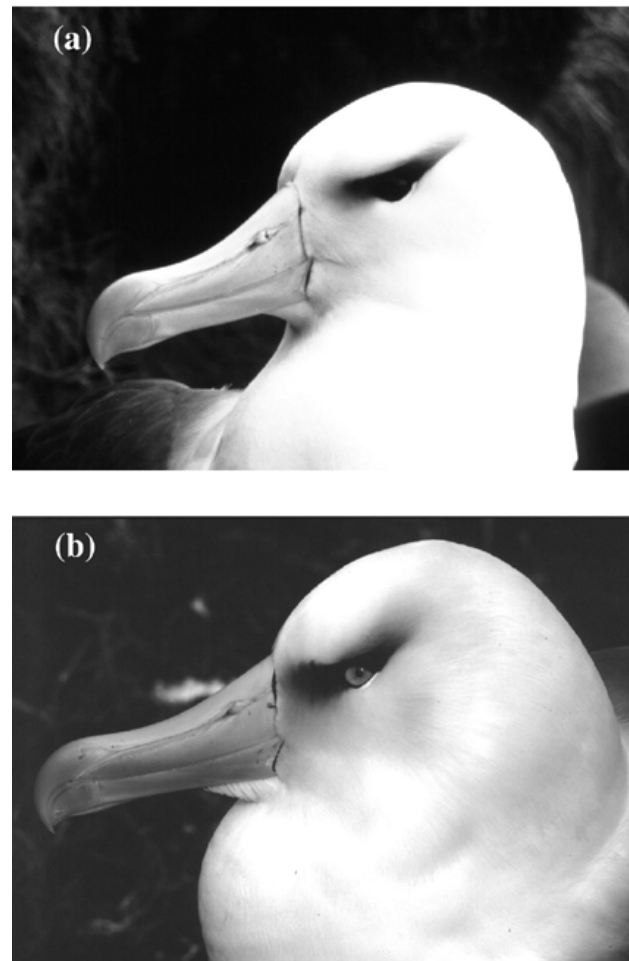


Fig. 2. (a) Black-browed Albatross on Campbell Island photographed in 1995, probably the male Falkland Islands *T. melanophrys* that was at the same nest in 1996. (b) Campbell Albatross, *T. impavida*, showing its distinctive light-coloured iris.

land, Bird and Campbell Islands (including the 18 dark-eyed birds) were screened against the primers to identify their species. To test the reliability of this PCR screening, 56 of the samples that had been sequenced from those three islands were amplified and the resulting banding patterns were compared.

DNA was extracted using a Chelex extraction protocol modified from Walsh *et al.* (1991). PCR was performed in 25- μ L reaction volumes containing 200 μ M dNTP, 1.5 μ M MgCl₂, 5 pmol each primer and 0.2 units *Taq* (Hybaid) in a 1 \times Hybaid reaction buffer. For each sample three PCRs were conducted using one of the H400 primers (H400TmFI 5'-CGAGCACTGCCGTATATTGTCAG-3', H400Tm 5'-CGAGCACTGCCGTATATTGCTGA-3' or H400 TiC 5'-CGAGCACTGCCGTATGCRGCTGG-3') and L-ND6* (5'-CCACCCATAATACGGCGAAGG-3', modified from Quinn and Wilson (1993)). The thermal profile was one cycle at 120 s at 94°C, 45 s at 50°C, 120 s at 72°C; six cycles at 60 s at 94°C, 45 s at 50°C, 90 s at 72°C; 25 cycles at 60 s at 93°C, 30 s at 55°C, 60 s at 72°C; and one final cycle at 300 s at 72°C. PCR products were visualised by electrophoresis on a 1% agarose gel. Birds were classified into one of the three groups on the basis of the presence of a single band, approximately 600 bp in length, from one of the three PCR reactions.

Results

Eye colour and taxon

Of the 30 birds that had light-coloured irises, 29 tested positively as *T. impavida*. For the remaining sample it was not possible to amplify its mtDNA using any of the primers. Of 15 dark-eyed birds, nine were *T. melanophrys*, three were Falkland Islands *T. melanophrys* and three were *T. impavida*. Three birds with intermediate iris colour were *T. impavida* on the basis of the results of the the H400 primer screening.

Sex and breeding pairs

Eight out of nine *T. melanophrys* and two out of three Falkland Islands *T. melanophrys* were males. Seventeen breeding pairs are depicted schematically in Fig. 3 on the basis of eye colour and taxon. Not shown is a male *melanophrys* whose partner was not seen at the nest (hence its eye colour was unknown) and a female *melanophrys* that was apparently a non-breeder. Two light-eyed and one dark-eyed bird were not identified to species (shown as ? in Fig. 3) because no blood samples were taken, or in one case the mtDNA tests failed repeatedly. A third light-eyed partner is included in Fig. 3 because, although not seen in 1996, it was paired in previous years to the same dark-eyed bird. Five (71%) out of seven male *melanophrys* were paired with dark-eyed partners (including a bird with intermediate iris colour) but none of their female partners was the same taxon as the male (Fig. 3).

The remaining male *melanophrys* and Falkland Islands *melanophrys* were paired with light-eyed *impavida* (Fig. 3).

Measurements

The measurements of birds sampled in 1996 are summarised in Table 1. Sample sizes are small, especially for the two forms of *T. melanophrys*, and generally there is overlap between the taxa for each measurement. An ANOVA comparing each measurement for the three types was run separately for males and females with no significant results. The result for bill tip (maximum vertical measurement) in females was almost significant ($F = 3.9$, d.f. = 2, $P = 0.056$). *T. impavida* females tended to be smaller than their *melanophrys* counterparts in most measurements, but males were smaller only in bill length (Table 1). The *impavida* with darker eyes fell within the range of measurements of the light-eyed birds, except for the male, which had a particularly long bill (Table 1).

Discussion

Of 18 dark-eyed Black-browed Albatrosses that were sampled for blood in 1996, 11 were banded and their breeding had been monitored between 1984 and 1995 (Moore *et al.* 1997). The other seven were banded in 1996. Although they were assumed to be Black-browed Albatrosses (Moore *et al.* 1997), this paper shows that there were three forms of dark-eyed birds: *T. melanophrys*, Falkland Islands *T. melanophrys* and *T. impavida*. Probably dark-eyed birds number fewer than 100 individuals amongst the many thousands of Campbell Island Albatrosses (Moore *et al.* 1997).

One explanation for Campbell Island having representatives of all presently identified types of Black-browed and Campbell Albatrosses is that there is a low level of interchange amongst all colonies. Further evidence of this is that two types were found on the Falkland Islands, with 14% of birds having *T. melanophrys* mtDNA, but only *T. melanophrys* was found at the other three islands sampled (Burg 2000). Albatrosses make long foraging trips and non-breeding migrations to and from their breeding areas (Warham 1990), which explains why banded Black-browed Albatross from most island groups have been recovered in Australasian waters (Marchant and Higgins 1990). Albatrosses are highly philopatric to natal colonies, so there are few examples of colony interchange. However, not all birds return to their natal colonies to breed and this allows for range expansion and

| | | | | | | | | | | | | | | | | | |
|--------|---|---|---|---|---|---|---|---|-----|---|-----|---|---|---|---|---|-----|
| Male | I | I | I | I | I | I | I | I | FIM | M | FIM | M | M | M | M | M | M |
| Female | I | I | I | I | I | I | I | ? | ? | ? | I | I | I | I | I | ? | FIM |

Fig. 3. Schematic depiction of breeding pairs of Black-browed Albatross on Campbell Island based on eye colour: light (no shading), intermediate colour (dark grey) and dark (light grey); and taxon: *T. impavida* (I), Falkland Island *T. melanophrys* (FIM), *T. melanphrys* (M) and no sample (?).

recovery of populations from catastrophic events (Warham 1990). Examples include an adult *T. melanophrys* breeding on Heard Island that was originally banded as a chick on Kerguelen Island (Woehler 1989), and Wandering Albatrosses, *D. exulans*, that have shifted islands (Warham 1990). Another example is a *T. melanophrys* breeding on Campbell Island that was originally banded as an adult of undetermined status on Macquarie Island (Moore *et al.* 1997). However, whether this bird was reared on Macquarie Island is unknown.

Banding studies and sightings have shown that movements of *T. impavida* adults and juveniles are largely restricted to the south-west Pacific (Marchant and Higgins 1990; Waugh *et al.* 1999). Recent band recoveries reveal that some *T. impavida* and Falkland Islands *T. melanophrys* from Campbell Island travel to South America (Moore and Battam 2000) but no Campbell Island birds are known to have colonised other islands. *T. impavida* should be obvious on the other islands, although the eye colour is noticeable only at close range and could easily be overlooked in large colonies.

The evolution of a distinctive form of Campbell Albatross may be the result of this phenotype being more successful than other Black-browed Albatrosses in the New Zealand region, or as a result of a long period of isolation. Other petrels are known to have recolonised previous breeding ranges (Warham 1990) but currently there is no general pattern of expansion of Black-browed Albatrosses as populations are variously increasing, stable or decreasing (Gales 1998), even within the same island group (Croxall *et al.* 1998). **A recent colonisation of the south-west Pacific Ocean seems likely as colonies on Campbell, Macquarie and Antipodes Islands and The Snares all have fewer than 120 breeding pairs of Black-browed Albatrosses (Copson 1988; Clark and Robertson 1996; Gales 1998; Tennyson *et al.* 1998) and the species was apparently absent in the early 1900s (Copson 1988; Tennyson *et al.* 1998). Breeding was**

first reported in 1949 on Macquarie (Copson 1988), suspected in 1950 (Warham and Bell 1979) and confirmed in 1978 on Antipodes (Clark and Robertson 1996) and 1984 on The Snares (Tennyson *et al.* 1998).

The *T. melanophrys* and Falkland Island *T. melanophrys* found on Campbell Island had a sex ratio skewed toward males, resulting in few opportunities for intraspecific pairings. This could have been caused by a sex imbalance in the source populations or differing migration patterns between the sexes, as suggested by Moore *et al.* (1997). For some other petrels, such as Manx Shearwaters, *Puffinus puffinus* (Brooke 1990), or Royal Albatross, *Diomedea epomophora* (Robertson 1993), females are the principal migratory sex. This is thought to be because male philopatry increases their chances of obtaining territories, whereas female migration avoids the chance of inbreeding (Warham 1990). The opposite would appear to be the case on Campbell Island. Alternatively, the sex imbalance of *T. melanophrys* on Campbell Island could be a result of differential mortality caused by fisheries bycatch. For example, foraging ranges of female Wandering Albatrosses, *D. exulans*, overlap with high fishing activity and result in lower survival than males (Weimerskirch and Jouventin 1987; Weimerskirch *et al.* 1997). Similarly, disproportionate numbers of female Grey Petrels, *Procellaria cinerea*, are caught in New Zealand fisheries (Bartle 1990, 2000; Murray *et al.* 1993; Robertson 2000). The sex ratio of Black-browed Albatrosses caught in Australian waters is even (Gales *et al.* 1998) but the small numbers caught in New Zealand waters are slightly biased towards females: 2 males:5 females (Murray *et al.* 1993), 8:10 (Bartle 2000) and 0:2 (Robertson 2000). Although these differences are small, annual survival of female Wandering Albatross at a level only 1% lower than males was enough to explain a large population decline and sex imbalance over a 16-year period (Weimerskirch *et al.* 1997).

Table 1. Measurements of Albatrosses on Campbell Island, grouped according to taxon

I = *T. impavida*, M = *T. melanophrys*, FIM = Falkland Islands *T. melanophrys*; int. = intermediate colour; m = male, f = female; bill length, bill max. = maximum bill depth, bill min = minimum bill depth (Sagar *et al.* 1998); bill tip = depth of bill at the tip (maximum vertical measurement through the maxillary angulus); mid toe = length of middle toe; and tarsus = length of tarsus (standard for procellariiforms: Marchant and Higgins 1990)

| Sp. | Characteristics | | | Measurement (mean \pm s.d., in mm) | | | | | |
|-----|-----------------|-----|----------|--------------------------------------|----------------|----------------|----------------|-----------------|----------------|
| | Eye | Sex | <i>n</i> | Bill length | Bill max. | Bill min. | Bill tip | Mid toe | Tarsus |
| I | Light | M | 6 | 113.8 \pm 2.6 | 48.1 \pm 1.5 | 28.0 \pm 0.5 | 30.7 \pm 0.7 | 122.7 \pm 1.2 | 88.3 \pm 1.8 |
| I | Int. | M | 1 | 113.0 | 49.0 | 28.4 | 30.8 | 126.5 | 88.0 |
| I | Dark | M | 1 | 122.9 | 49.1 | 28.7 | 31.2 | 122 | 91.6 |
| I | All | M | 8 | 114.8 \pm 4.0 | 48.3 \pm 1.3 | 28.1 \pm 0.5 | 30.8 \pm 0.6 | 123.1 \pm 1.7 | 88.7 \pm 1.9 |
| I | Light | F | 7 | 112.6 \pm 2.8 | 46.2 \pm 1.4 | 26.5 \pm 1.4 | 28.7 \pm 0.9 | 120.8 \pm 3.3 | 84.3 \pm 1.5 |
| I | Int. | F | 2 | 113.3 \pm 5.5 | 46.8 \pm 2.8 | 27.0 \pm 0.4 | 29.3 \pm 0.1 | 120.2 \pm 4.7 | 86.4 \pm 4.2 |
| I | Dark | F | 2 | 115.1 \pm 0.3 | 46.9 \pm 0.5 | 26.4 \pm 0.4 | 28.7 \pm 0.3 | 118.3 \pm 0.5 | 86.0 \pm 1.0 |
| I | All | F | 11 | 113.2 \pm 3.0 | 46.4 \pm 1.4 | 26.5 \pm 1.1 | 28.8 \pm 0.7 | 120.2 \pm 3.1 | 85.0 \pm 2.0 |
| M | Dark | M | 7 | 117.2 \pm 2.9 | 48.5 \pm 1.6 | 28.4 \pm 1.2 | 30.6 \pm 1.1 | 122.3 \pm 3.4 | 87.0 \pm 2.0 |
| FIM | Dark | M | 2 | 119.7 \pm 6.4 | 48.0 \pm 0.8 | 27.1 \pm 0.1 | 30.9 \pm 0.8 | 124.5 \pm 1.9 | 87.9 \pm 0.6 |
| M | Dark | F | 1 | 118.3 | 48.3 | 27.3 | 29.3 | 119.1 | 86.8 |
| FIM | Dark | F | 1 | 114.5 | 48.3 | 27.6 | 30.9 | 121.7 | 87.5 |

In all, 71% of *T. melanophrys* males on Campbell Island bred with dark-eyed females of some sort, suggesting that they selected preferentially for dark-eyed birds if partners of the same type were not available. This preference is particularly evident when it is considered that dark-eyed birds were extremely rare amongst the numerous light-eyed *T. impavida*. This is shown further by birds with multiple partners. For example, one of the dark-eyed *T. impavida* × *T. melanophrys* pairs bred together from 1992 to 1996. Prior to that they each had bred with other dark-eyed birds. In contrast, though, another male *T. melanophrys* bred with three different light-eyed birds from 1987 to 1996. The latter could be an example of a vagrant becoming associated with, and imprinted to, a more numerous but similar species rather than seeking its own kin (Warham 1990) or simply a result of the skewed sex ratio and lack of suitable partners.

Courtship between albatross species is probably common, hence there is a mechanism for cross-breeding. This is well known in the crowded mixed-species colonies of the Hawaiian islands; however, there are no definite examples of viable hybrid young being produced there and they are rare in other petrels (Warham 1990). An exception is the recruitment of hybrids of crosses between Southern, *D. epomophora*, and Northern Royal Albatrosses, *D. sanfordi*, at Taiaroa Head (Robertson 1993).

It is not known whether the three dark-eyed and three intermediate dark-eyed *T. impavida* on Campbell Island were hybrids or had natural variation in eye colour. If eye colour is inherited by simple Mendelian ratios and the genes for dark eyes are dominant, then first-generation hybrids would have dark eyes (or intermediate colour) and their offspring would include some light-eyed birds. As mitochondrial DNA is inherited maternally, male *T. melanophrys* × female *T. impavida* crosses would therefore produce hybrids with *T. impavida* mtDNA and have dark irises. Female *T. melanophrys* × male *T. impavida* crosses would have *T. melanophrys* mtDNA but would be indistinguishable from pure *T. melanophrys* because of their dark eyes. However, because there are so few female *T. melanophrys* on Campbell Island and none currently has an *T. impavida* mate, there may be few or no cryptic hybrids present. The presence of hybrids is possible since, although most interbreeding pairs had low breeding success in 1984–95, several pairs produced flying young (Moore *et al.* 1997). For example, one of the Falkland Islands *T. melanophrys* males bred with the same light-eyed *T. impavida* from 1991 to 1996 and fledged chicks on at least four occasions. However, until some of these young are found as adults their appearance is a matter of conjecture.

Although the first dark-eyed individual was not seen until 1975, some adults that were monitored between the 1980s and 1996 had been banded as chicks as early as 1970 as part of a cohort-banding programme at the albatross colonies (Moore *et al.* 1997). They were not noted at the time as anything unusual since both *T. melanophrys* and *T. impavida* chicks have dark

irises (Marchant and Higgins 1990). Two known-age dark-eyed birds were identified during our study as *T. impavida*. Assuming they are hybrids, mixed-species pairings must have occurred on Campbell Island since 1970 or earlier.

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References

- Bartle, J. A. (1990). Sexual segregation of foraging zones in procellariiform birds: implications of accidental capture on commercial fishery longlines of Grey Petrels (*Procellaria cinerea*). *Notornis* **37**, 146–150.
- Bartle, J. A. (2000). Autopsy report for seabirds killed and returned from New Zealand fisheries 1 October 1996 to 31 December 1997. Department of Conservation, Conservation Advisory Science Notes No. 293.
- Brooke, M. (1990). 'The Manx Shearwater.' (T. and A. D. Poyser: London.)
- Burg, T. M. (2000). Genetic analyses of albatrosses: mating systems, population structure and taxonomy. Ph.D. Thesis, University of Cambridge, Cambridge.
- Clark, G., and Robertson, C. J. R. (1996). New Zealand White-capped Mollymawks (*Diomedea cauta steadi*) breeding with Black-browed Mollymawks (*D. melanophrys melanophrys*) at Antipodes Islands, New Zealand. *Notornis* **43**, 1–6.
- Copson, G. R. (1988). The status of the Black-browed and Grey-headed Albatrosses on Macquarie Island. *Papers and Proceedings of the Royal Society of Tasmania* **122**, 137–141.
- Croxall, J. P., Prince, P. A., Rothery, P., and Wood, A. G. (1998). Population changes at South Georgia. In 'Albatross Biology and Conservation'. (Eds G. Robertson and R. Gales.) pp. 69–83. (Surrey Beatty: Sydney.)
- Fridolfsson, A. K., and Ellegren, H. (1999). A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* **30**, 116–121.
- Gales, R. (1998). Albatross populations: status and threats. In 'Albatross Biology and Conservation'. (Eds G. Robertson and R. Gales.) pp. 20–45. (Surrey Beatty: Sydney.)
- Gales, R., Brothers, N., and Reid, T. (1998). Seabird mortality in the Japanese tuna longline fishery around Australia, 1988–1995. *Biological Conservation* **86**, 37–56.
- Griffiths, R., Daan, S., and Dijkstra, C. (1996). Sex identification in birds using two CHD genes. *Proceedings of the Royal Society, London* **263**, 1251–1256.
- Griffiths, R., Double, M. C., Orr, K., and Dawson, R. J. G. (1998). A DNA test to sex most birds. *Molecular Ecology* **7**, 1071–1075.
- Kahn, N. W., St John, J., and Quinn, T. W. (1998). Chromosome-specific intron size differences in the avian CHD gene provide an efficient method for sex identification in birds. *Auk* **115**, 1074–1078.
- Marchant, S., and Higgins, P. J. (Eds) (1990). 'Handbook of Australian, New Zealand and Antarctic Birds. Vol. 1A. Ratites to Petrels.' (Oxford University Press: Melbourne.)
- Moore, P. J., and Battam, H. (2000). Procellariiforms killed by fishers in Chile to obtain bands. *Notornis* **47**, 168–169.
- Moore, P. J., Taylor, G. A., and Amey, J. M. (1997). Interbreeding of Black-browed Albatross *Diomedea m. melanophrys* and New Zealand Black-browed Albatross *D. m. impavida* on Campbell Island. *Emu* **97**, 322–324.

- Murray, T. E., Bartle, J. A., Kalish, S. R., and Taylor, P. R. (1993). Incidental capture of seabirds by Japanese Southern Bluefin Tuna longline vessels in New Zealand waters, 1988–1992. *Bird Conservation International* **3**, 181–210.
- Quinn, T. W., and Wilson, A. C. (1993). Sequence evolution in and around the mitochondrial control region in birds. *Journal of Molecular Evolution* **37**, 417–425.
- Robertson, C. J. R. (1993). Timing of egg laying in the Royal Albatross (*Diomedea epomophora*) at Taiaroa Head 1937–1992. Department of Conservation, Conservation Advisory Science Notes No. 50.
- Robertson, C. J. R. (2000). Autopsy report for seabirds killed and returned from New Zealand fisheries 1 January 1998 to 30 September 1998. Department of Conservation, Conservation Advisory Science Notes No. 294.
- Robertson, C. J. R., and Nunn, G. B. (1998). Towards a new taxonomy for albatrosses. In 'Albatross Biology and Conservation'. (Eds G. Robertson and R. Gales.) pp. 13–19. (Surrey Beatty: Sydney.)
- Sagar, P. M., Stahl, J. C., and Molloy, J. (1998). Sex determination and natal philopatry of Southern Buller's Mollymawks (*Diomedea bulleri bulleri*). *Notornis* **45**, 271–278.
- Sambrook, J., Fritsch, E. F., and Maniatis, T. (1989). 'Molecular Cloning: a Laboratory Manual.' 2nd Edn. (Cold Spring Harbor Laboratory Press: New York.)
- Seutin, G., White, B. N., and Boag, P. T. (1991). Preservation of avian blood and tissue samples for DNA analyses. *Canadian Journal of Zoology* **69**, 82–90.
- Tennyson, A., Imber, M., and Taylor, R. (1998). Numbers of Black-browed Mollymawks (*Diomedea m. melanophrys*) and White-capped Mollymawks (*D. cauta stadi*) at the Antipodes Islands in 1994–95 and their population trends in the New Zealand region. *Notornis* **45**, 157–166.
- Turbott, E. G. (Ed.) (1990). 'Checklist of the Birds of New Zealand and the Ross Dependency, Antarctica.' 3rd Edn. (Random Century: Auckland.)
- Walsh, P. S., Metzger, D. A., and Higuchi, R. (1991). Chelex 100 as a medium for PCR based typing from forensic material. *Biotechniques* **10**, 506–513.
- Warham, J. (1990). 'The Behaviour, Population Biology and Physiology of the Petrels.' (Academic Press: London.)
- Warham, J., and Bell, B. D. (1979). The birds of Antipodes Island, New Zealand. *Notornis* **26**, 121–169.
- Waugh, S. M., Sagar, P. M., and Cossee, R. O. (1999). New Zealand Black-browed Albatross *Diomedea melanophrys impavida* and Grey-headed Albatross *D. chrysostoma* banded at Campbell Island: recoveries from the South Pacific region. *Emu* **99**, 29–35.
- Weimerskirch, H., and Jouventin, P. (1987). Population dynamics of the Wandering Albatross, *Diomedea exulans*, of the Crozet Islands: causes and consequences of the population decline. *Oikos* **49**, 315–322.
- Weimerskirch, H., Brothers, N., and Jouventin, P. (1997). Population dynamics of Wandering Albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biological Conservation* **79**, 257–270.
- Woehler, E. J. (1989). Resightings and recoveries of banded seabirds at Heard Island, 1985–1988. *Corella* **13**, 38–40.

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