INTERSPECIFIC BREEDING IN GIANT PETRELS AT SOUTH GEORGIA.

INTRODUCTION

The existence of two broadly sympatric sibling species of giant petrels *Macronectes* was first reported by Bourne & Warham (1966). The Northern Giant Petrel *M. halli* breeds at the sub-antarctic islands north to the Chatham Islands, New Zealand, while the Southern Giant Petrel *M. giganteus* breeds at most sub-antarctic islands and south to the Antarctic Peninsula and Continent. The taxonomic status of the birds breeding at Gough Island and at the Falkland Islands has been in doubt (Johnstone *et al.* 1976), but recent data confirm that they are a well marked form of *M. giganteus* (Devillers & Terschuren 1980; Voisin & Bester 1981; Voisin unpubl.).

Where breeding populations of the two species co-exist (at Marion, Crozet, Macquarie, Heard and South Georgia Islands) *M. halli* consistently breeds about six weeks earlier than *M. giganteus* (Bourne & Warham 1966; Voisin 1968). This difference in the timing of breeding is thought to be an important reproductive isolating mechanism and although a number of interspecific breeding attempts have been reported from Marion Island (Burger 1978), and Macquarie Island (Johnstone 1978) in no case has there been a report of eggs successfully hatching.

A three year study (1978-1981) of the comparative ecology of the two species of giant petrel at Bird Island (an island of *c.* 400 ha, at 54° 00′S, 38° 02′W, off the north-west end of South Georgia) has provided the most extensive information yet available on interspecific breeding in giant petrels.

METHODS

About 1,500-1,800 pairs of giant petrels (*c.* 1,000-1,200 pairs *M. halli* and 500-650 pairs *M. giganteus*) normally breed at Bird Island, though in some seasons, such as 1980-81, many pairs do not lay, or lose eggs early in the season and are not recorded during censuses. In each season *c.* 350 nests were checked and the species of both adults determined and *c.* 250 nests were visited weekly to determine breeding success and hatching dates.

To identify species the criterion used was bill colour (Johnstone 1974; Voisin 1976). In *M. halli* the endplate or unguis of both mandibles is dark pink, tending to maroon at times. It contrasts strongly with the yellowish-horn colour of the rest of the bill. In *M. giganteus* the unguis of each mandible is pale green and the bill looks uniform in coloration from a distance.

In both species birds were sexed using bill length (Murphy 1936; Conroy 1972). Birds with bills over 97 mm in length were classed as males, whilst those under 95 mm were classed as females. The few birds occuring in the overlap zone (94-97 mm) were sexed by reference to the sex of their mate.

RESULTS

Table I shows the incidence of interspecific pairings recorded at Bird Island, 1978-81. Interspecific pairings were of two distinct types. In Type A a male *M. giganteus* was paired to a female *M. halli*; in Type B a male *M. giganteus* was paired to a female bird that could not be specifically identified using bill colour. These birds had bills that were a weak horn colour throughout, lacking the dark red tip of *M. halli* or the pale green tip of *M. giganteus*. Chicks from both types of interspecific pair hatch at dates significantly different from and roughly intermediate between those of the two species (Table II). There is also a significant difference ($p < 0.05$) between the mean hatching dates of both interspecific pair types.

All six chicks from the type A pairs fledged successfully; four of the nine chicks from type B pairs fledged successfully. All these chicks showed the plumage characteristic of both *M. halli* and *M. giganteus* fledglings, but had a bill rather paler and less yellowish than *M. halli* chicks and lacking both the reddish tip that some of these show and the green tip of *M. giganteus* chicks.

Where a pair was found breeding in a second or third season the birds had retained their original partners. Two pairs were located for three consecutive seasons and two pairs for two consecutive seasons.

TABLE I

Number of giant petrel pairs at Bird Island

Season	Giant petrel population (pairs) Total	Checked	Hybrid pairs Type A[1]	Type B[2]	Total	Percentage of pairs checked
1978-79	*c.* 1,800	408	1	2	3	0.74
1979-80	*c.* 1,550	284	3	4	7	2.46
1980-81	*c.* 1.200	265	2	3	5[3]	1.89

Notes: 1. *M. giganteus* ♂ x *M. halli* ♀ 2. *M. giganteus* ♂ x indeterminate ♀ 3. Excludes one type A pair that did not lay.

TABLE II

Giant petrel hatching dates at Bird Island

Taxon	Number	Mean	S.D. (days)	Range
M. halli	98	30 Nov.	4	22 Nov. - 11 Dec.
M. giganteus	191	10 Jan.	4	30 Dec. - 23 Jan.
M. giganteus ♂ x *M. halli* ♀	4	13 Dec.[1]	10	28 Nov. - 20 Dec.
M. giganteus ♂ x *indet.* ♀	6	26 Dec.[2]	4	23 Dec. - 3 Jan.

Notes: 1. Difference from *M. halli* significant at $p < 0.02$, from *M. giganteus* at $p < 0.001$ ('t' test).
2. Differences from *M. halli* and *M. giganteus* significant at $p < 0.001$.

DISCUSSION

About 1.5% of the breeding pairs of giant petrels at Bird Island involve interspecific breeding. While this is a small proportion it is not insignificant and, although we lack fully comparable data from other sites, may well be greater than at Marion Island (2 interspecific pairs in 1,490; 0.1%; Burger 1978) or Macquarie Island (1 interspecific pair in *c.* 5,000; 0.02%; Johnstone 1978).

It is certain, however, that the interspecific pairs at Bird Island are fully capable of producing and raising offspring. Furthermore I suggest that the indeterminate females in type B pairs are the progeny of interspecific matings. They are intermediate in bill colour between the two species and breed at a date significantly different from either species. If they are hybrids then they are clearly fertile and capable of rearing a chick.

There are two important questions to be discussed. First, why (and how) does hybridization occur? Second, why are hybrid birds not being eliminated from the breeding population?

Occurrence of Hybridization

All known pairings at all localities have involved a male *M. giganteus* paired to a female *M. halli* (Burger 1978; Johnstone 1978; this study) or to an indeterminate female (this study). This is presumably because any unpaired female *M. halli* (whether young prospective breeders or older birds that have lost mates) that are still seeking partners once the majority of the *M. halli* has commenced breeding are more likely to encounter males of *M. giganteus,* rather than *M. halli,* that are in breeding condition. This would account for a timing of breeding that is essentially intermediate between the two species. By contrast, later in the season, female *M. giganteus* without mates are most unlikely to encounter *M. halli* males, because of the preponderance of male *M. giganteus* at this time, even if the former were still in reproductive condition. Just as in normal pairs, interspecific pairings, once established, maintain their pair-bond over several seasons. No adult male birds of indeterminate species were found, despite the occurrence of male hybrid chicks. The reason for this is unknown.

At Bird Island interspecific contact is facilitated by the large population of both species on a small island and their consequent close proximity as both breeding and non-breeding birds. Mixed-species groups of off-duty and displaying birds are frequently seen and the situation is totally unlike that prevailing at the Crozet Islands, where no interspecific association was recorded (Voisin 1978) and apparently dissimilar to that at Marion Island where there is only a very small population of *M. halli* (Burger 1978). At Bird Island the population of *M. halli* has increased substantially over the last twenty years in parallel with the increase in Antarctic fur seals *Arctocephalus gazella* (Croxall & Prince 1980). The existence of large numbers of inexperienced and unpaired young birds might also lead to an increased likelihood of hybridization.

Maintenance of Hybridization

The difference in the timing of breeding in *M. halli* and *M. giganteus* might maintain ecological as well as reproductive isolation. Although giant petrels are basically opportunist feeders with broad dietary tastes (Hunter in press) there are nevertheless some consistent dietary differences between the species at Bird Island that are associated with the timing of breeding. Thus *M. halli* chicks hatch during the period of maximum availability of fur seal bull carcasses and pup corpses and placentae (Hunter in press). In contrast, *M. giganteus* rarely feeds at seal carcasses at Bird Island. One might expect individuals breeding at intermediate times to be at a disadvantage compared with those breeding at normal times.

However, at present food may be sufficiently abundant to permit breeding at such times.

As the number of fur seals at Bird Island is still increasing, *M. halli* continues to benefit from increasing food availability. It may not be coincidental that type A interspecific pairs breed at a time closer to that of *M. halli* than *M. giganteus,* presumably profiting thereby from access to fur seal material. Nevertheless timing of breeding is presumably also strongly influenced by the proximate reproductive condition of the individual which will be influenced by arrival date at the breeding site and the progress of courtship thereafter. It is not surprising, therefore, that type B interspecific pairs, in which I suggest that 75% of genes come from *M. giganteus,* should breed at a time closer to *M. giganteus* pairs than to those of *M. halli.*

Predation of chicks at Bird Island is virtually unknown. Therefore the generally favourable food conditions, perhaps especially for *M. halli* and type A hybrids, are presumably responsible for the success of interspecific pairs in rearing chicks at a time intermediate between the breeding seasons of the two species. Apart from the relatively small number of birds available for mating at such times, there does not appear presently to be any obvious selection against interspecific matings and one would predict a gradual increase in the incidence of hybridization at Bird Island.

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