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THE PAIR BOND IN PENGUINS AND PETRELS; A BANDING STUDY

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The present paper is a detailed study of the Yellow-eyed Penguin, *Megadyptes antipodes* (Hombron and Jacquinot), extending over a decade from August, 1936 to May, 1946. It was carried out on the Otago Peninsula, New Zealand. In all 973 visits were paid to the several colonies which are 20 miles from the city of Dunedin with the outermost 20 miles apart. The range of the species is very much restricted, reaching from the northern side of the Otago Harbour, 45° 45's, to Campbell Island, 52° 35's. A perusal of a map will indicate that there is very little land in this area.

The observations here summarized concern 88 male and 96 female penguins which were found breeding for a minimum of one season. In addition, 31 of these males in one or more seasons were unmated after having once bred. Since practically all of the penguins returned to the same area year after year some 292 matings between male and female were recorded.

All birds were securely marked with aluminum bands which had to be evolved and made by me. In addition, any individuals required for special observation were marked with colored celluloid bands for quick identification.

This is the first time a survey has been made of banded penguins in the wild state from one season to the next. As a result of the research several papers have already been published (1940, 1941a, 1941b, 1945, 1946). As well as these a lengthy treatise on "Sexual Behaviour in Penguins" is nearing completion.

In addition to the above, a banding study was made into the length of the pair bond in five species of petrels—*Pelecanoides urinatrix* (Gmelin), *Pachyptila turtur* (Kuhl), *Pelagodroma marina* (Latham), *Puffinus griseus* (Gmelin), and *Diomedea epomophora sanfordi* Murphy (Royal Albatross). The first three were studied for five years, the fourth for three, and the last for ten years. The first four species were

examined on the tiny island of Whero, off the south-east corner of Stewart Island and the Royal Albatross on the extreme tip of the Otago Peninsula not far away from the *Megadyptes* colonies.

LENGTH OF THE PAIR BOND IN MEGADYPTES

This species is not a migratory penguin like *Pygoscelis adeliae* (Hombron and Jacquinot), but comes ashore at its own particular breeding area at periodic intervals during the winter months. It is at this stage that most of the pairs are formed although this phenomenon may be initiated at any period during the annual cycle. In other words, when *Megadyptes* begins to stay ashore during the daytime to perform behavior patterns which precede egg deposition, the great majority of the pairs are already formed. Because of this fact it is obviously not necessary that a male should mate with a female whose sexual rhythm synchronizes with his own. Pair-formation acts independently of the oestrus condition. Since there is a 24.9 percent excess of breeding males, counting all birds of both sexes over two years of age, it is a rare occurrence for a breeding female to be left unmated.

Briefly, *Megadyptes* does not mate for life although there is a tendency for mated pairs, if each member returns, to remain together. This happens in 82 percent of the cases. The causes of a dissolution in partnership are death, disappearance, and "divorce."

TABLE I
ANNUAL SURVIVAL OF MATED PAIRS

Year	Pair broken because of				Pair remains intact	
	loss of one or both birds		"divorce" of one or both birds			
	number	percent	number	percent	number	percent
1937-38	5	62½	—	—	3	37½
1938-39	8	29	7	25	13	46
1939-40	18	50	5	14	13	35
1940-41	11	42	1	4	14	54
1941-42	6	25	3	12½	15	62½
1942-43	6	20½	4	14	19	65½
1943-44	5	19	4	15	17	66
1944-45	7	22	2	6	23	72
1945-46	16	41	4	10	19	49
Total	82	33	30	12	136	55

TABLE 2
DURATION OF PAIRING BOND

Years	Number of pairs	Years	Number of pairs	Years	Number of pairs
1	48	3+	10	6	2
1+	42	4	2	6+	3
2	13	4+	1	7	—
2+	19	5	2	7+	1
3	10	5+	4		
				Total	157

N. B. A plus sign means that the mated pair was in existence either when the first observation was made or was still a fact when the final observations closed.

Table 1 signifies that out of 248 matings in nine years, 136 or 55 percent remained intact in the succeeding season. Eighty-two, or 33 percent of the pairs were dispersed owing to death or disappearance of one or both members of the pair. Thirty, or 12 percent were separated owing to "divorce." This figure represents 18 percent of the total of 166 pairs which returned to breed again in the succeeding year in the same colony. In 17 of these instances both members of the "divorced" pair remated with other penguins and in 13 cases one member of the old pair was left unmated. All of the latter except two were males. These are the only two occasions on which females have remained without a partner and occurred in the tenth year of study. The circumstances, however, were somewhat unusual.

Of the 82 partnerships which were broken because of loss, in 16 both birds disappeared and in 66 only one returned. Of these, 41 mated with other birds and 25, all males, were left unemployed for at least one season. This means that in 38 instances birds were left unemployed at least one season after having mated.

Table 2 gives some idea of the length of time the pairs remain intact. Of the 292 matings recorded for the ten years, 157 distinct groupings of pairs were involved. Seventy-seven of these groupings lasted from one to six years exactly for an average of 1.7 years. The status of each of these birds was known prior to pair-formation and it was also known when the partnership was dissolved.

Regarding the balance of the groupings, 80 in all, the pair was either an accomplished fact when the records began or was still in existence during the tenth year of study. These pairs have lasted, to my knowledge, from one to seven years, with an average of two years, which in actual practice would be much higher. The seven, one of the six, all of the five, and the four-year spans are still intact.

TABLE 3

FURTHER DATA ON RETENTION OF PAIRS

Number of birds which nested		Male	Female	Total
once	and not seen again	7	22	29
twice	" " " "	10	17	27
three times	" " " "	6	5	11
four	" " " "	5	3	8
five	" " " "	3	2	5
six	" " " "	2	2	4
seven	" " " "	2	1	3
eight	" " " "	—	2	2
nine	" " " "	1	—	1
Total		36	54	90
once	and not lost	23	10	33
twice	" " " "	3	8	11
three times	" " " "	6	6	12
four	" " " "	2	1	3
five	" " " "	4	4	8
six	" " " "	4	4	8
seven	" " " "	4	1	5
eight	" " " "	5	2	7
nine	" " " "	1	6	7
Total		52	42	94

Table 3 indicates that mortality among the females appears to be much greater and this is particularly noticeable in the first two lines of the table when 39 females were lost as against 17 males. It should be remembered that there is always a surplus of males in any colony. Many of these have mated only once, a fact that has greatly augmented the male total in the first line of the second half of the table. The last line indicates that six females have nested nine times and are still in the colony. There are also nine males which have been present for nine years and one for ten years but all except two have been unmated for one or more seasons (see also Table 4).

Thirty-six male and 54 female penguins have not been seen again in their nesting colony after the pair was broken. One or two of these have reappeared elsewhere but this is a rare occurrence. I firmly believe that most of the disappearances are due to death. The bodies of eight males and eleven females have been recovered. This is just over 21 percent of the total that has disappeared. Since the chances of recovering bodies are small, the figure 21 percent surely signifies that many of the other missing penguins died.

TABLE 4

SPAN OF PAIR BOND IN ALL BIRDS KNOWN FROM 7 TO 10 YEARS

♂	Span of pair bond	Years	♂	Span of pair bond	Years
721	+1, 1, 1, 2u, 3, 2+	10	692	+7u, 1+	8
1	+1, 1, 3, 3u, 1+	9	X10	3u, 2, 1, 1u, 1+	8
3	+1, 5, 1u, 2+	9	40	+1, 6—	7
15	+2, 2u, 5+	9	51	+1u, 1, 2, 1u, 2—	7
20	+1, 1, 3u, 3—	9	52	1u, 5, 1u—	7
28	+3, 1, 3u, 1, 1+	9	155	5u, 1, 1+	7
34	+6, 1u, 1, 1+	9	675	4u, 3+	7
37	+1u, 2, 1, 5+	9	683	1u, 2, 2u, 1, 1+	7
39	+6, 3+	9	720	2u, 3, 2+	7
72	+1, 4, 3, 1—	9	738	7+	7
21	+1, 1, 4, 1u, 1—	8	W18	2u, 1, 1, 3+	7
36	+2, 6+	8	Z13	+1, 1, 1u, 4+	7
42	+2, 3, 2u, 1—	8	Z14	+1u, 1, 2u, 1, 2+	7
64	+1, 3, 1u, 3+	8	B20	+1u, 1, 1, 1, 1, 1u+	6
102	+2, 1u, 5+	8	Total	29♂♂	
♀			♀		
2	+6, 2, 1+	9	73	+2, 1, 2, 3—	8
4	+1, 1, 5, 1+	9	75	+2, 2, 1, 3—	8
18	+2, 3, 3, 1+	9	76	1, 6, 1—	8
25	+2, 1, 1, 5+	9	116	+3, 1, 4+	8
27	+6, 3+	9	B13	6, 1+	7
35	+1, 1, 3, 3, 1+	9	618	6+	6
16	+1, 7+	8	Total	13♀♀	

Key:

- +1 etc. means mated for one year etc., and previous status unknown.
- 1+ etc. means pair still in existence.
- 1u etc. means unmated for one season etc.
- 1— etc. means mated for one season etc. and then lost or dead.

A study of Table 4 manifests considerable variation in retention of mates. The male 721 had, in ten years, five mates and was twice unmated. The male 39 had two mates only in nine years and his only break in partnership was due to "divorce." Another male, 738, had only one mate in the seven years. The male B20 had a different status each of the six years under observation. Only five of the 29 males listed have not passed a season mateless within my knowledge. Two of these extended for nine years, one of which is still in the colony. One male, 692, was seven consecutive years unmated before acquiring a mate.

Of the females not one has been left unmated. Bird 35 had five partners in nine years and five of the others have had four mates. Female 618, which produced eggs as a two-year-old and is a daughter of the male 3, had only one mate (36) and is still living.

With such frequent changes of partners as manifested by Table 4 one would expect to find the remating of several pairs after "divorce." Seven years passed without anything of this nature occurring. In 1943-44, B20 and 78, which had been mated in 1941-42, again mated after having been separated and mated to other birds in the intervening year. The partnership did not hold, for in 1944-45, B20 mated with 76, and 78 with 721.

The second case is of considerable interest for it is a continuation of a story already published (1946: appendix a). Briefly, the male 20 showed an affinity towards the female 18 in the winter of 1939 and the pair spent much time together when ashore. In the spring, however, 18 mated with the male 1. For three years these two remained mated and 20 lived nearby unmated. Then in 1942-43 the rôles of the males were reversed. Male 20 mated with 18 and male 1 became the odd member of the trio and remained nearby also unmated. This new association lasted another three years when 20 died during the moult of 1945. That spring bird 1 again mated with his old partner 18 close to their old nest.

LENGTH OF THE PAIR BOND IN OTHER PENGUINS

There are no data available for the other species of penguins comparable with that which has been supplied for *Megadyptes*. Even though taken from birds in captivity the findings of Gillespie (1932: 95-130) probably reflect what actually happens in the wild state. Table 5 gives the annual matings as far as can be ascertained from his book.

A careful study of the table will indicate how closely the mating arrangements of *Aptenodytes patagonica* J. F. Miller resemble those of *Megadyptes*. The former, likewise, does not mate for life but there is a tendency for mated pairs to remain together for a period. One male, in seven years was mated each season and had three different mates resembling very much such males as 39, 72, and 37 in *Megadyptes*. One case of remating after a "divorce" was recorded.

TABLE 5

ANNUAL MATINGS OF APTENODYPTES PATAGONICA
GILLESPIE (1932: 95-130)

	Mated birds	Egg date	Unmated birds
1918	Charles & Ann	8 July	Bertrand, Dora, Erica
1919	do	1 Sept.	do
1920	do	10 July	do
1921	Charles & Erica	6 June	Ann
	Bertrand & Dora	7 June	
1922	Charles & Dora ¹	15 June	Erica ¹ Ann
	Bertrand & Dora	1 Aug.	
1923	Charles & Dora	18 June	Ann
	Bertrand & Erica	2 July	
1924	Charles & Dora	10 June	Erica died
	Bertrand & Ann	24 June	
1925	?		
1926	?		Charles died
1927	Bertrand & Dora		Ann

¹Could Erica possibly have laid this egg?

In regard to the remaining species there is evidence that in at least two of them mates may be retained from one season to the next. This has been noted by me in *Eudyptes sclateri* Buller (1941b) and *Eudyptula minor* (J. R. Forster) (unpublished observations). Regarding the latter, information supplied by Hursthouse (1940: 121) seems to point in the same direction. The records cover only two consecutive seasons so that little is known about the duration of the bond or whether "divorces" obtain. It is suggested, however, that all species may conform to the pattern as set by *Megadyptes* and *patagonica*.

LENGTH OF THE PAIR BOND IN PETRELS

An examination will now be made of the length of the pair bond in petrels. Owing to the nature of the terrain and the consequent difficulties in recovering species nesting in burrows it was not possible to obtain results with the same degree of accuracy as with *Megadyptes* and the Royal Albatross. In Table 6, therefore, many of the figures preceding a plus sign would in practice be much greater. Further in all five species many of the pairs were found together either before or after a successful breeding season. These occurrences are not included in the table which deals only with birds with eggs or chicks.

TABLE 6

DURATION OF PAIR BOND IN PETRELS

Years	Number and percentage of pairs				
	<i>Pelecanoides urinatrix</i>	<i>Pachyptila turtur</i>	<i>Pelagodroma marina</i>	<i>Puffinus griseus</i>	<i>Diomedea e. sanfordi</i>
1	15 (10.2)	8 (4.4)	7 (3.6)	6 (6.4)	1 (12.5)
1+	87 (59.6)	118 (65.2)	142 (73.6)	86 (91.5)	
2	2 (1.4)				
2+	26 (17.8)	28 (15.5)	25 (12.9)	2 (2.1)	
3	1 (.7)	1 (.5)			
3+	8 (5.5)	14 (7.8)	14 (7.3)		1 (12.5)
4					1 (12.5)
4+	6 (4.1)	9 (4.9)	5 (2.6)		
5+	1 (.7)	3 (1.7)			
6+					1 (12.5)
8+					1 (12.5)
9+					1 (12.5)
10+					2 (25.0)
Total	146	181	193	94	8
Percent- age more than one year	30.2	30.4	22.8	2.1	87.5

N. B. Percentages in brackets.

In *Megadyptes* the percentage of mated pairs which remained intact for more than one season lies between 42.7 and 69.4 (Table 2). Since it is definitely known that 115 pairs in the proportion of 48 to 67, mated either for one year only or for more than one there are 42 pairs whose status is in doubt. They mated at least once. Working on this proportion it may be assumed that 18 of these 42 mated for only one year and 24 for more than one. On this basis the real percentage which mated for more than one year would be 54.1.

In the first three petrels noted the percentage is lower than this but in actual practice it would be much higher. In *Puffinus griseus* the survey had not progressed far enough but the tendency is for the same pattern to be followed. Quite a number of pairs were found again together in the succeeding season but without eggs or chicks. As regards the Royal Albatross, it seems to follow a different pattern and it appears that the pairs may mate for life, for there has not been a single "divorce." There was one case of remating after one of the partners had disappeared (1942: 175, 262).

It would seem from the above that the length of the pair bond in the four burrowing petrels noted is very similar to that in *Megadyptes*. This is further supported by the fact that instances of "divorce" have been discovered in all four, although not to the same extent as in *Megadyptes*. Obviously, there must have been others which were not found. "Divorce" in these species is therefore not an exceptional affair.

As regards other petrels the evidence where available appears to run on similar lines. Roberts (1940: 158), watching for two successive seasons, indicates that Wilson's Petrel (*Oceanites oceanicus* (Kuhl)) tends to remain mated from season to season. Lockley (1942: 105, 322) working on wider observations thinks that the Manx Shearwater (*P. p. puffinus* (Brünnich)) mates for life and that although "divorces" occur these are exceptional. Finally, behaviour very similar to that of *P. griseus* was observed by Lewis (1924: 87) on 44 banded birds of a closely allied species, *P. tenuirostris* (Temminck). One pair was found together for three consecutive years.

DISCUSSION

The length of the pair bond in birds varies considerably from those like the Ruff (*Philomachus pugnax* (Linné)) in which the sexes meet solely for coition to those like some of the Anatidae which mate for life. Lack (1940: 269-272) has analyzed these variations into five classes. His fourth class deals with the species which remain paired either for a single brood and then separate as in the House Wren, *Troglodytes aedon* Vieillot (Baldwin, 1921: 237-238), or for one season before separating. The tendency is for the majority of this class to adopt the latter course (Nice, 1930: 70-72, 1937: 88, 1943: 182). That there may be considerable variation from this rule is well illustrated by Kendeigh (1941: 55). Lack's fifth class is composed solely of birds which mate for life.

Megadyptes would seem to lie midway between these two groups. In this species 82 percent of the mated pairs which return, remain intact for the second season. These partnerships may then continue for as long as seven consecutive years. This fact means there is an 18 percent "divorce" rate which is an important and influencing feature in the duration of the pair bond. Moreover change of mates is not accidental as in Lorenz's Jackdaws (Lack, 1940: 271). This type of pair bond obviously does not fit into either of Lack's two classes. It is therefore necessary to establish an extra category in which are placed species that tend to remain mated for some years and in which there is a definite element of "divorce."

Judging by the evidence which has been presented concerning *Atenodytes patagonica*, *Eudyptes sclateri*, and *Eudyptula minor* it is quite possible that the other species of penguins also belong to this new

group. Such a possibility would at least be a fruitful source for research. It would seem also that some of the petrels are in this class and that the Royal Albatross and perhaps other Diomedidae are possibly exceptions.

To what extent other birds mate for a period before "divorce" intervenes needs further investigation. It is not an easy matter to trace the partners after separation, especially if the birds are numerous or widely dispersed. Terns and gulls may behave according to the pattern being discussed. Tinbergen (1939: 228) has noted the return of two out of seven pairs of gulls four years in succession but no "divorces." The same may apply to many of the Paridae (Odum, 1941: 317-318) in which one case of "divorce" has been reported (Kenrick, 1940: 309).

To sum up, it would seem that in addition to *Megadyptes* and probably at least some of the other species of penguins, that several species of petrels and some other birds like the Paridae, gulls, and terns may belong to the proposed new class of length of the pair bond. They tend to remain mated for some time and "divorce" is more than a chance occurrence.

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RECOVERIES OF BANDED LEACH'S PETRELS¹

BY ALFRED O. GROSS

The Leach's Petrel (*Oceanodroma leucorhoa leucorhoa* (Vieillot)) nests on isolated islands, usually those located well out to sea that are difficult to visit and where landings may be hazardous when rough seas prevail. In nesting the petrel digs a long burrow, which facilitates the task of capturing the adults, but it requires a bander of unusual enthusiasm and energy to excavate a large number of the nests. For these reasons comparatively few petrels, only about 4,000, have been banded, but from these we have 116 recoveries which are the basis of this preliminary report. I am indebted to Frederick C. Lincoln of the U. S. Fish and Wildlife Service and to various cooperators for permission to use their records.

Leach's Petrel is a common nesting species on certain islands of the Grand Manan Archipelago, Bay of Fundy, New Brunswick, Canada, and on islands along the coast of Maine. In the Bay of Fundy region petrels have been banded on Kent, Southern Green, Outer Wood and Machias Seal islands. Kent, a member of a group generally designated as Three Islands, is the site of the Bowdoin Scientific Station. It is located about six miles southeast of Seal Cove, Grand Manan. Southern Green Island is one and a half miles directly north and Outer Wood Island is three miles northwest of Kent Island. Machias Seal Island, the site of a lighthouse station, lies well out to sea about ten miles southwest of Southern Head Light, Grand Manan.

Kent Island has a diversity of conditions of terrain varying from open grassed areas and swamps to others grown up with a thick growth of virgin spruce. A few of the petrel burrows are in the open areas and in places littered with fallen dead spruces at the southern end,

¹Contribution Number 16, Bowdoin-Kent Island Scientific Station, Kent Island, Bay of Fundy, New Brunswick, Canada.