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BREEDING AND MORTALITY OF THE SOUTH ISLAND ROBIN IN KOWHAI BUSH, KAIKOURA

By R. G. POWLESLAND

ABSTRACT

The breeding of the South Island Robin at Kowhai Bush, Kaikoura, during the 1977-78 and 1978-79 seasons and the mortality from August 1976 to December 1979 are described. Most robins began laying in August and completed breeding in January. Thirty-four percent of their nests were relined " old " ones built in previous seasons by robins or *Turdus* species. Average time to build a " new " nest was 3.4 days, followed by a prelay period that averaged 4.2 days.

Eggs were laid at about 24-hour intervals. Mean clutch size was 2.7 eggs (range 2-4), being smallest in July and largest in October. Incubation averaged 17.7 days, and the females spent 81% of daylight time on the eggs; males did not incubate. In the two seasons, 63% of the eggs hatched and 23% were eaten by predators. Hatching success varied between seasons, months and the four age classes of females.

Both parents fed the nestlings, but only the female brooded. Nestlings averaged 20.8 days in the nest, with little or no brooding after day 15. Overall, 42% of the nestlings fledged; most of the rest were eaten by predators. The proportion that fledged decreased as the season progressed because the loss to predators increased. Pairs fledged a mean of 2.1 fledglings in 1977-78 and 2.9 in 1978-79.

Juveniles were fed by their parents from 24 to about 50 days, depending on the number of juveniles, how many the female cared for and how soon the next clutch hatched.

Mortality was highest in summer for immatures and autumn for adults. Immatures died more in summer, possibly because they were less efficient foragers than adults, but similar proportions of the two age classes died in autumn and winter, perhaps because predation was the main mortality factor.

INTRODUCTION

The South Island Robin *(Petroica australis australis)* is very suitable for detailed observations of breeding biology because it is approachable and its nests can be found readily (Soper 1976). Moncrieff (1932), Richdale (1941), Oliver (1955), Soper (1976) and Falla *et al.* (1978) made general observations of the species' breeding habits, and J. A. D. Flack studied its behaviour, breeding success and mortality at Kowhai Bush and on several offshore islands (Flack 1973, 1976a and b, 1979; Flack & Lloyd 1978).

During a study of the Robin's annual time-budget at Kowhai Bush, I recorded breeding behaviour and success for the 1977-78 and 1978-79 breeding seasons. In addition, monthly censuses were made of the individually colour-banded and known-age robins.

STUDY AREA

Kowhai Bush (40°54'S, 174°05'E) is in coastal south-eastern Marlborough, 7 km inland from Kaikoura. It is a narrow (700-1700 m wide) 240-ha strip of forest on the north-eastern side of the Kowhai River, 60-150 m a.s.l. The forest is a flood-induced series of successional stages of varying age, structure and species composition, often dominated by kanuka *(Leptospermum ericoides)* (Dobson 1979). For a detailed account of the geology, climate, flora and fauna of the study area, see Hunt & Gill (1979).

METHODS

I watched pairs at the nest from about 7 m away. Nests were visited daily to determine the dates of nest building, laying, hatching and fledging, and every second or third day during incubation and nestling rearing to check for predation.

Eggs were measured with vernier calipers to the nearest 0.1 mm and, the day they were laid, weighed with a spring balance to the nearest 0.1 g.

Each nestling was given an individual combination of a metal serial band and colour bands at about 13 days of age. Robins which immigrated into the study area were caught with a clap-trap or mist net and banded. I defined juveniles as young that had left the nest but were still being fed by their parents. Juveniles became immature robins once they were independent of parental care, and remained so until the start of breeding in late July.

To calculate the mean date robins began breeding each season I averaged the dates of the first egg laid by all females. When a laying date was not known it was estimated from the day of hatching, allowing 18 days for incubation.

The robin's breeding cycle was divided into six stages:

1. Nest building: From when the female first made repeated visits to a site with nest material and carried out " nest-shaping " movements (the female crouches into the nest cup, pushing outward with her wings and, apparently, scratching backward with her feet) to when she made fewer than 1 trip per hour to the nest with material.

2. Prelay: From the completion of the nest to the day before the first egg was laid.

3. Laying: Those days when an egg was laid and time spent incubating was less than 50%.

4. Incubation: From the first day the female spent more than 50% of her time incubating to the hatching of the first egg.

5. Nestling rearing: From the hatching of the first egg until the last nestling left the nest.

6. Juvenile rearing: From the day the nestlings left the nest to their independence.

Each month a record was kept of each banded robin seen. Towards the end of each month those not seen were searched for in their territories. Outside the breeding season (January to July), I sought banded robins beyond the study area. Only two dead adult robins were found, but many more disappeared. Therefore, to determine robin mortality. it was inferred that when a bird disappeared from the study area it had died. Adults in Kowhai Bush were very sedentary; few that had lived there were subsequently found elsewhere. Thus, if an adult disappeared it had probably died. However, if an immature disappeared I could not confidently assume its death because some immatures dispersed long distances.

RESULTS

Breeding season

The mean date that first eggs were laid was 16 August in 1977-78 (n = 27) and 13 August in 1978-79 (n = 13). The mean dates for the two years do not differ significantly (P>0.05). The mean date for both seasons was 15 August (range 23 July-1 September). Since nest building and prelay together lasted an average of 11 days in August, the mean date robins began nest building was 4 August. Three-year-old females had the earliest mean date of starting to lay, followed by 2-year-olds, 1-year-olds and lastly those 4 years and older

TABLE 1 — Mean date of laying of first eggs of the breeding season for female South Island Robins of four age classes. Combined data from the 1977-78 and 1978-79 seasons

Female age	Mean date of laying	N	SD
1 year	15 Aug	15	10.4
2 years	14 Aug	7	11.3
3 years	7 Aug	6	12.3
4 years and older	18 Aug	12	9.7

(Table 1). When the mean dates of starting to lay are statistically compared for the various age classes of females, only those for 3-year-olds and those 4 years old and older were significantly different ($P<0.05$).

The last clutches of the season were laid in early January. Pairs that hatched such late clutches and fledged the nestlings were still feeding juveniles in March. Therefore, a few pairs were breeding for over 7 months. However, most late eggs or nestlings were eaten by predators, and so most breeding finished by late January.

Nest sites

Common sites were trunk and branch forks, mistletoe *(Loranthus micranthus)*, crowns of kanuka and in old *Turdus* and robin nests. Of 164 nests found in the two seasons, only once was a female known to re-use the same nest for successive clutches; she relined the nest between clutches. Thirty-four percent of the 164 nests were old nests of robins, Song Thrushes *(Turdus philomelos)* and Blackbirds *(T. merula)* made in previous seasons, which the robins relined. The proportion of nests per month that were old decreased towards the end of the breeding season: 36% of 11 in July, 54% of 35 in August, 35% of 20 in September, 38% of 32 in October, 21% of 43 in November and 17% of 23 in December ($P<0.001$).

The mean height of the 164 nests was 3.7 m (range 0.8-8.7 m) in a forest with a 5-12 m high canopy. Flack (1973) recorded nests as low as 0.5 m and as high as at least 11.0 m. There was a significant difference between the mean height of new robin nests (mean = 4.0 m, n = 109) and relined old ones (mean = 3.0 m, n = 55) (t = 3.29, d.f. = 162, $P<0.01$). Song Thrushes and Blackbirds built nests lower (mean = 2.2 m, n = 47) than did robins (t = 5.77, d.f. = 154, $P<0.001$).

Nest building

This was done solely by the female. On average she made 22.4 trips per hour with material to the nest (117 hours of observation) but the building rate decreased as the nest neared completion. Most

material was collected within a 50-m radius, usually from the ground and off tree trunks but sometimes from old robin and *Turdus* nests. While females built nests their mates fed them on average 3.2 times each hour (89 hours of observation).

Three stages were discernible in the building of a new nest. Firstly, coarse materials such as rootlets, twigs and strips of bark were brought to the site and bound together with cobwebs. Next, the nest was lined with finer material, particularly mosses, but no cobwebs were used. Finally, a thin layer was added of very fine material such as mosses, fern scales, dried grasses, papery bark, leaf skeletons and occasionally a few down feathers. The cups of completed nests were often full of this material which had not been pressed into place.

New nests took a mean of 3.4 days to build (range 2-6 days, n = 27). However, nest building sometimes took longer because females occasionally abandoned sites after building in them for several hours, once for 2 days. The sites abandoned were often so open that material kept falling out of them when the bird made nest-shaping movements. If it rained heavily soon after building began, females had difficulty forming the base of the nest. The coarse material did not bind together, perhaps because the cobwebs were wet. Although I found no females starting to build in old nests, this relining seemed to take less than a day. The number of days taken to complete a new nest decreased during the season: 4.8 days for 5 nests in July, 4.5 for 4 in August, 3.0 for 6 in September, 2.6 for 5 in both October and November, and 2.5 for 2 in December $(P > 0.5)$.

Although most pairs were capable of raising three broods a season, many pairs built more than three nests to replace clutches eaten by predators. Over the two breeding seasons, 40 females built

TABLE 2 — Mean length (days) of the prelay stage, the frequency of clutch sizes and the mean clutch size for robins in each month of the breeding season. Combined data from the 1977-78 and 1978-79 seasons

		Prelay stage		Frequency of clutch sizes			Mean clutch size
	N	Mean length	Range	2	3	4	
Jul	4	6.8	8-5	4	-	-	2.0
							NS*
Aug	12	5.1	6-4	28	8	-	2.2
							P < 0.001
Sep	5	4.8	7-3	1	19	-	2.9
							NS
Oct	5	3.6	4-3	1	27	2	3.0
							P < 0.05
Nov	13	2.9	4-2	7	29	1	2.8
							NS
Dec	5	3.6	5-2	7	16	-	2.7

• NS = not significant

and laid in an average of 4.1 nests (new and old) per season. Twelve females built 3 nests each, 14 built 4, 11 built 5 and 3 built 6.

Prelay

This lasted on average 4.2 days (range 2-8 days, n = 44). The monthly mean duration varied, being longest in July and shortest in November (P>0.7, Table 2). The male continued to feed his partner regularly during this stage, but only 1.5 times per hour (48.3 hours of observation), half the rate of that to females building nests.

Laying

This stage lasted for only 1 or 2 days because most clutches were of two or three eggs, eggs were laid at 24-hour intervals and full incubation began the day the last egg was laid. Most eggs were laid within 3 hours of sunrise. On two occasions an egg was laid several days after the previous one. A third case involved an egg being laid in a nest containing nestlings 10 days old. Twice, the first egg of a clutch was preyed on in the afternoon or night after it had been laid without shell or yolk being left in the nest or the nest cup being dishevelled. The subsequent eggs of these birds were also eaten within 24 hours of being laid in the same nests.

Females with incomplete clutches spent 13.8% of daylight time on their eggs (31.6 hours of observation). During the laying stage they were fed, on average, 2.5 times per hour by their partners (35.0 hours of observation), nearly twice as often as during the prelay stage.

The ovoid eggs were variously coloured, ranging from white without any markings to pale brown with brown, purplish brown, or black blotches and spots evenly distributed over them. Most eggs were chalky white with brownish markings concentrated at the larger end. The mean length and maximum breadth ($\pm$ SD) of 363 eggs were 24.9 $\pm$ 0.10 mm and 18.6 $\pm$ 0.04 mm, extremes being 21.8 x 18.2 mm, 28.2 x 18.4 mm, 26.6 x 17.6 mm and 24.0 x 20.0 mm. The mean fresh weight of 126 eggs was 4.5 $\pm$ 0.27 g. Since the average weight of 18 adult female robins was 35.1 g in spring (J. A. D. Flack, pers. comm.), the mean egg weight represents 12.9% of the female's body weight. This is slightly above the average of 10% for a passerine of that body weight (Lack 1968: 184).

The mean clutch sizes for the two seasons (1977-78: mean 2.74 $\pm$ 0.51, n = 100; 1978-79: mean 2.62 $\pm$ 0.49, n = 50) do not differ significantly (t = 1.39, 148 d.f., P>0.05). Thus, the two seasons' data were combined, giving a mean of 2.70 eggs per clutch. The monthly mean clutch size changed during the course of the breeding season (Table 2). From no 3-egg clutches in July, the proportion increased to a maximum in October, and then declined. Flack (1979) found the same monthly trend of mean clutch size in his earlier study of the Kowhai Bush robin population. The mean clutch sizes of the four age classes of female robins did not differ significantly for their

TABLE 3 — Frequency distribution and means of clutch sizes for the four age classes of female robins for the first clutches of the breeding season, and for all clutches laid during the season. Combined data from the 1977-78 and 1978-79 seasons

| Age class | Frequency distribution and means of | | | | | | | |
| | First clutches | | | | All clutches | | | |
	2	3	4	Mean	2	3	4	Mean
1 year	12	3	-	2.2	21	36	1	2.7
2 years	6	1	-	2.1	10	16	-	2.6
3 years	4	2	-	2.3	5	16	1	2.8
4 years and older	8	4	-	2.3	12	31	1	2.7

first clutches of the season or for all clutches laid during the breeding season (Table 3).

Incubation

Only the female robin incubated. Females became fully attentive (i.e. spent about 80% of time incubating) the day they laid their last egg, but after August some did so the day they laid the penultimate egg of 3-egg and 4-egg clutches. On average, they spent 81.0% of daylight time incubating (236 hours of observation). Incubation lasted 17 (n = 10 clutches), 18 (n = 19) or 19 days (n = 1), with a mean of 17.7 days. Similarly, Flack (1979) found that the robins incubated for about 18 days.

In total, males made 2.5 visits per hour with food to their incubating partners (236 hours of observation). However, this rate depended on whether the male was feeding juveniles from a previous nest (1.1 visits per hour, 58 hours of observation) or not (2.9 visits per hour, 178 hours of observation). Incubating females that received food less often incubated less (78% of 58 hours) than did those that were fed at the higher rate (83% of 178 hours, $P<0.01$).

Table 4 shows that 63% of robin eggs hatched and 23.3% were eaten by predators. According to the evidence left at the nest (Flack & Lloyd 1978), stoats *(Mustela erminea)* and weasels *(M. nivalis)* took 88.3% of the eggs eaten and ship rats *(Rattus rattus)* and house mice *(Mus musculus)* took the rest.

Nearly 22% more eggs hatched in 1978-79 than in 1977-78, mainly because fewer eggs were preyed on in 1978-79 (Table 4). From the combined results for the two seasons, fewer eggs were abandoned, remained unhatched or had unknown fates as the season progressed, but predation increased. Clutches were abandoned most often in bad weather, particularly when heavy rain and strong winds continued for 2 or 3 days. If the female disappeared (died) during incubation, the clutch was abandoned, but if a male disappeared, the female continued incubating (n = 3). Unhatched eggs included those that were infertile

TABLE 4 — The fates of South Island Robin eggs (% of total laid) in total, and on the basis of breeding season, month, and female age

	No. of eggs	Egg fates (%)					
		Preyed on	Fell from nest	Abandoned	Unhatched	Unknown	Hatched
Total	405	23.2	1.5	3.9	6.2	2.2	63.0
Season							
1977–78	274	29.5	2.2	3.3	6.6	2.9	55.5
1978–79	131	11.3	0.0	5.2	5.3	0.8	77.4
Month							
Jul	8	0.0	0.0	0.0	25.0	12.5	62.5
Aug	80	2.5	3.7	7.5	7.5	5.0	73.8
Sep	59	0.0	0.0	5.1	11.8	1.7	81.4
Oct	91	22.0	3.3	3.3	6.6	2.2	62.6
Nov	105	38.1	0.0	1.9	2.9	0.9	56.2
Dec	62	53.1	0.0	3.1	1.6	0.0	42.2
Female age							
1 year	154	26.6*	3.9	2.6	7.1	2.6	57.2
2 years	68	8.8	0.0	5.9	5.9	1.5	77.9
3 years**	62	43.6	0.0	4.8	6.5	4.8	40.3
4 years and older	121	16.5	0.0	4.1	5.0	0.8	73.6

* Apparent large differences in the proportion of eggs preyed on from the female age categories are not real. The female age categories were unevenly represented in the two seasons when predation levels differed
** Not present during the 1978-79 season

or in which the embryo died during development. More eggs remained unhatched early in the season because some complete first clutches were infertile.

Three-year-old females hatched 40.3% of their eggs, significantly fewer than the other three age categories did (P<0.05, Table 4). This apparent poor ability of 3-year-old females to hatch eggs is not real because there were no females of this age in the 1978-79 season, when a smaller proportion of eggs were preyed on than in the previous season. One-year-olds hatched a smaller proportion of their eggs than did 2-year-olds (P<0.05) and those 4 years old and older (P<0.05). In general, a similar proportion of eggs from the four female age classes was abandoned, remained unhatched or had unknown fates. Two 1-year-old females lost eggs because of unstable nests, which fell from their sites.

Nestlings

A brood usually took from a few hours to a day to hatch. Once nestlings were present, the male brought food mostly to the young instead of to the female. However, while the nestlings were 1-3 days old, he sometimes passed food to the female, which then fed it to the young. During heavy rain, when the female spent most of her time sheltering the nestlings, she occasionally accepted food

from the male while on the nest, rather than move aside to let the nestlings be fed.

Only the female brooded nestlings. In general, females brooded for about 80% of daylight time when the nestlings were 1-2 days old. The amount of brooding gradually declined as the nestlings aged, and when about 15 days old, they were not brooded during the day. Nestlings left the nest after an average of 20.8 days (range 19-22, n = 19 broods). Three broods that fell from collapsed nests when 12, 15 and 16 days old were fed on the ground until they could fly.

For both seasons combined, similar percentages of nestlings were preyed on (46.3%) or fledged (42.0%) (Table 5). Of the rest (11.7%), nearly equal proportions fell from the nest and died, died in the nest, or had unknown fates. By the criteria of Flack & Lloyd (1978), mustelids took 94% of the nestlings preyed on and rodents took the rest. Thus of the eggs and nestlings eaten, mustelids took a slightly greater proportion of nestlings than eggs (P>0.05).

Between the two seasons, there was no significant difference in the proportion of nestlings that were preyed on, fell from the nest and died, died in the nest, had unknown fates or successfully left the nest (Table 5). Of the completed clutches (i.e. those not preyed on during laying) and broods, 61.3% were eaten in 1977-78 (n = 119) and 48.2% in 1978-79 (n = 54). This difference between the seasons is significant (P<0.05) and may reflect a change in predator numbers between the seasons. These figures are within the range (44-66%)

TABLE 5 — The fates of South Island Robin nestlings (% of total) in total, and on the basis of breeding season, month, and female age

| | No. of nestlings | Nesting fates (%) | | | | |
		Preyed on	Fell from nest and died	Died in nest	Unknown	Fledged
Total	255	46.3	3.5	3.9	4.3	42.0
Season						
1977-78	152	48.0	2.0	3.3	4.6	42.1
1978-79	103	43.7	5.8	4.8	3.9	41.8
Month						
Jul	5	0.0	0.0	0.0	0.0	100.0
Aug	59	11.9	3.4	16.9	3.4	64.4
Sep	48	35.4	4.2	0.0	4.2	56.2
Oct	57	54.4	7.0	0.0	7.0	31.6
Nov	26	61.5	0.0	0.0	7.7	30.8
Dec	27	77.8	3.7	0.0	0.0	18.5
Female age						
1 year	88	50.0	7.9	2.3	6.8	33.0
2 years	53	48.1	3.8	1.9	3.8	43.4
3 years*	25	32.0	0.0	8.0	0.0	60.0
4 years and older	89	46.1	0.0	5.6	3.4	44.9

*Not present during the 1978-79 season

of the proportion of robin nests whose contents were preyed on during the six previous breeding seasons at Kowhai Bush (Moors & Flack 1979).

,' Fewer nestlings fledged and more were preyed on from month to month (Table 5). Similarly, the proportion of nestlings whose fates were unknown increased during the season, except in December. The proportion that died in the nest or that died after falling from the nest shows no obvious monthly trend.

In 1977-78, 30 pairs averaged 2.1 fledglings per pair. In 1978-79, 15 pairs averaged 2.9 fledglings per pair. Over the five seasons 1971-2 to 1975-6, Flack (1976b) found that robins fledged on average 3 fledglings per pair each season.

Three-year-old females fledged the greatest proportion of nestlings, but the difference was not significantly greater than that for the other age classes (Table 5). One-year-old females raised fewer nestlings than did either 2-year-olds ($P < 0.05$) or those 4 years old and older ($P < 0.05$).

Juveniles

On leaving the nest, juveniles had short tails, a few down feathers on the crown, flew poorly, and perched at one place for several hours. However, by a fortnight after leaving the nest they flew proficiently, following an adult about and quickly flying to it for food when called. At this age they began foraging, mainly on the ground.

In the five known cases, male and female robins each fed particular juveniles. This division of the brood seemed to happen within the first week of leaving the nest. When the number of juveniles was odd, the male usually took care of the extra one. Once the female began nest building, and certainly by the time she started incubating, the male fed all juveniles.

The number of days parents fed juveniles varied greatly. Juveniles whose parents renested were fed usually until the next clutch hatched, which varied according to the number of juveniles present, how many the female cared for and how soon the next clutch hatched. When there was only one juvenile, the male took sole charge of it ($n = 12$), and the female often started to build her next nest within 3 days of the juvenile having left the nest. The single juvenile was often fed for a few days after the clutch hatched but was then driven from the territory, having received only about 24 days of parental care since leaving the nest. At the other extreme, females that cared for two juveniles sometimes delayed renesting for up to 35 days, or if their next clutches were preyed on, the juveniles were fed for up to 50 days before being ousted from the territory (Flack 1979, pers. obs.).

Mortality

Immatures: In 1979, and for the combined 1978 and 1979 data, mortality was highest in summer (Fig. 1). From the combined data, more immatures disappeared per month in summer than did adults (P<0.05), but in autumn and winter the differences were not significant (Table 6). Of the 118 juveniles produced in the two breeding seasons (Fig. 1), only 16.9% (8 males and 12 females) were present at the start of their first breeding season. Flack (1979) found that the survival to first breeding was highly variable between years (10-90%). By comparison, for the period August 1977 to August 1979, an average of 38.6% of 114 adults survived annually during this study. Thus, although adult survival was greater than that of immatures (P<0.05), it was much lower than that recorded by Flack (1979) from 1971 to 1976, when it varied around 70% per annum.

Adults: In 1977, 1978 and the three years combined (total), adult mortality was highest in autumn and lowest in the breeding season (Fig. 1), as was found by Flack (1976b, 1979). For the combined years' data, a similar proportion of adult males and adult females died each season, except in winter (P<0.05), when a greater proportion of bachelors (unpaired adult males) (40% of 10) died than did paired adult males (13.3% of 60, P<0.05). In contrast, only 10.9% of 46 adult females died in winter.

TABLE 6 — Percentage of adult and immature robins that disappeared (died) per month in summer, autumn and winter for 1978 and 1979

Age	Summer	Autumn	Winter
Adult	6.2 (91)*	11.5 (74)	11.4 (57)
Immature	14.2 (118)	11.8 (34)	11.5 (26)

*Number alive at the start of the season

DISCUSSION

Breeding season

Like Flack (1973, 1979), I found that South Island Robins in Kowhai Bush regularly started laying in late July-August and that most pairs had finished breeding by late January. In addition, Flack recorded the laying of three clutches in May and June. This 6-month-long breeding season differs from the 3-4-month season (late August to November) for the robins on Outer Chetwode Island at the head of Pelorus Sound (J. A. D. Flack, pers. comm.). When some robins from the island were released on to nearby Motuara Island, which had had no robins, the transferred birds began laying from August to December (Flack 1975). The Outer Chetwode Island robins had a smaller territory size range (0.2-0.6 ha per pair) than did the Kowhai Bush robins (1-5 ha per pair). Therefore, the island pairs may have been prevented by limited food from laying earlier (Powlesland 1981).
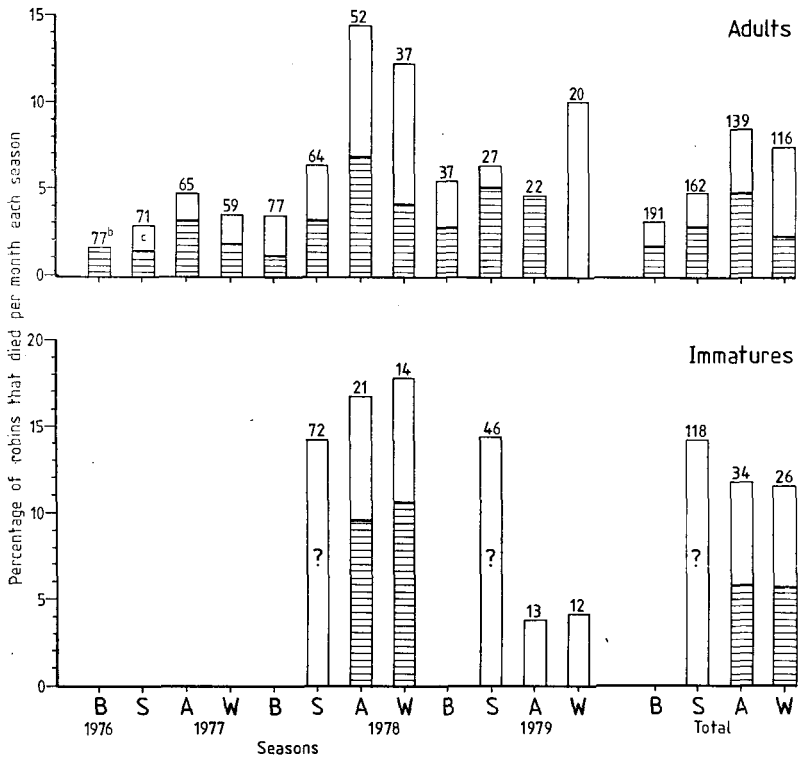
FIGURE 1 — The average percentage of adult and immature South Island Robins that died (disappeared) per month each season at Kowhai Bush from the 1976 breeding season to the 1979 winter and also in total.

B = breeding season (August-December)
S = summer (January-March for adults and November-March for juveniles)
A = autumn (April-May for both age classes)
W = winter (June-July for both age classes)

The figure above each column is the number of robins present at the start of each season.

The blank part of each column is the proportion of dead robins that were male and the cross-hatched part is the proportion that were female.

? = the proportion of males and females not known

  Robins were the first passerines to start breeding each year in Kowhai Bush. Several factors may have contributed to the early start. The robins' main prey, soil invertebrates, were apparently readily available in July and August. Their food storing (Powlesland 1980) may have enabled them to start breeding before Blackbirds and Song Thrushes, which also forage mainly on ground invertebrates in winter and spring. Male robins may have used food stored at times when prey was temporarily abundant to feed their mates and young when prey was less available. Also, female robins, unlike female Blackbirds and Song Thrushes (Witherby *et al.* 1938) are fed regularly by their mates while building nests, forming eggs and incubating.

Nests

  Old nests not only need less material and are quicker to build than new ones — only a few hours instead of several days — but also were of proven stability and strength. None fell or disintegrated while in use, but seven new nests did, with the loss of two clutches and two of five broods. Why the use of old nests declined as the season progressed is not known, but increased daylength may have enabled robins to build new nests more quickly later in the season than earlier. More trips with material to the nest site could be made per day in December, for example, than in August, and with warmer weather later in the season, feeding for maintenance may have needed less time, leaving more time for nest building.

Prelay

  During yolk formation in passerines most nutrients must be taken in, rather than derived from stored deposits in the body (Ankney & Scott 1980). Yolk formation in the robin occurs during nest building and prelay (pers. obs.). Thus, it is of note that females were fed less often by their mates in the prelay stage than when nest building. Two factors may explain this unexpected situation. Firstly, the robins foraged mainly by hopping over the ground and scanning from perches, activities which would be little hindered by the extra weight of developing eggs. Secondly, the female robins had time to forage for the extra food needed for egg formation. Time budgets showed that females hoarded surplus food and spent significantly more time resting and in body maintenance (preening, bathing, scratching and stretching) in the prelay stage than when nest building ($P<0.05$). Resting and body maintenance are low-priority activities and time spent in them was inversely related to that spent foraging (Powlesland 1981). Therefore, female robins during the prelay period were probably able to meet more of their food requirements than when nest building.

  The prelay period became shorter as the breeding season progressed probably because, with increasing daylength, females could forage longer each day and, needing less energy for maintenance in the warmer weather, could put more nutrients into egg formation. Also, with more hours of daylight, it was likely that a female received more food from her mate each day.

The greater mortality of bachelors in winter than of paired adult males may have been related to the significantly less time the bachelors foraged — 70% of 28.4 hours of observation and 90% of 54.9 hours of observation respectively ($P < 0.01$). The 20% extra time which paired adult males spent feeding, bachelors spent singing. Singing seemed to be to attract a mate because, once a bachelor robin became paired, he stopped almost all song. Therefore, if by singing so much bachelors spent only sufficient time foraging to meet daily maintenance requirements, perhaps their high mortality was because their bodily energy reserves were too low to sustain them during periods of bad weather. A study of the weight changes of bachelor and paired adult male robins during the non-breeding season might resolve this question.

Flack (1976b, 1979) considered that the regular increase of adult mortality in autumn was related to competition between adults and immatures for territories. The population in Kowhai Bush has been as high as 94 adults, but over the 3 years of this study it declined from 77 to 26. In late July 1981 only 16 robins (8 pairs) were present, compared with 23 (11 pairs and 1 bachelor) at the same time in 1980, the lowest counts since censuses were started in 1971. Thus, much of the forest formerly occupied by robins was unoccupied, leaving ample habitat for immature birds. The male establishes and defends the pair's territory. Therefore, if robin deaths in autumn were related to immatures competing for space with adults finishing their moult, more males would be expected to die than females. However, a statistically similar proportion of adult females (22.3% of 59) and adult males (12.5% of 80, $P > 0.05$) died in autumn.

Several other observations suggested that territorial disputes were not an important cause of the higher adult mortality in autumn during this study. No adult, male or female, was ousted from its territory or dominated by a non-territorial immature. The opposite occurred; any immature that trespassed on to the territory of an adult male that had completed his moult was chased to the boundary. Moulting adult males chased intruders, even if rather ineffectively, but not *vice versa*. Most immatures had territories by April. In summer and autumn, when adult males died immatures did not shift into the vacant territories, and so competition for " prime " habitat did not seem to be a factor in the mortality.

Adult mortality in autumn may have been caused by predators. Three adult female robins were killed on their nests by rodents in Kowhai Bush (Flack & Lloyd 1978). In addition, because robins were exterminated in only 2 years by ship rats on Big South Cape Island (Flack & Lloyd 1978) (and many robins live more than 4 years), rats can probably take roosting robins. As rodent populations reach peak numbers in autumn (Moors 1979), they may be responsible for some adult robin mortality. Flack & Lloyd (1978) concluded that rodents blundered on to nests while foraging but that mustelids were

active hunters. Therefore, mustelids can be expected to take more roosting birds than rodents and be the greater cause of adult robin mortality.

In 1976 the robins had contiguous territories, but by 1980 the population was in two parts with about half at each end of the study area. Immature birds seemed attracted to areas where other robins were present and took up territories near those of established birds. Although a 50-m wide floodway bisects Kowhai Bush, it did not directly divide the robin population. Robins flew over the floodway and immatures occupied habitat on the side opposite to their natal territory. If immature robins are attracted to areas where adults are present, this may explain the discontinuous distribution of robins in the South Island and their absence from seemingly suitable habitat between areas of occupied forest.

To identify the causes of higher adult mortality in autumn and thus the gradual decline of the Kowhai Bush robin population, the monthly mean weights of birds during the non-breeding season should show when they weigh least and so are most likely to die, directly or indirectly, from food shortages. In addition, the trapping of stoats, weasels and ship rats in the non-breeding season may show their role in robin mortality.

ACKNOWLEDGEMENTS

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SHORT NOTE

WELCOME SWALLOWS AT THE AUCKLAND ISLANDS

In early April 1983 I undertook a short tour of duty to the subantarctic islands in HMNZS *Otago.* On the approach to Enderby Island, in the Aucklands group, at 0930 on 11 April 1983, in company with P. Wilson and P. D. Gaze (Ecology Division, DSIR), we saw a flock of six Welcome Swallows flying towards the island. This was fairly close inshore at Sandy Bay, the weather being fair with some sun and little wind. Later, while ashore on Enderby Island I observed a single Welcome Swallow " hawking " overhead.

Dr M. W. Cawthorn (Fisheries Research Division, MAF), who was studying Hooker's Sealion on Enderby for 10 days before the above sightings, informs me that he had observed a flock of 20 Welcome Swallows working the cliffs and sward between East Bay and South East Point a few days earlier. He also had a record of the possible sighting of six swallows in the same area in late January 1982.

Apart from the 1943 record of the Welcome Swallow at the Auckland Islands mentioned in the New Zealand checklist and the field guide, these appear to be the only published records of the species at the Aucklands.

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THE LESSER PETRELS OF ANTIPODES ISLANDS, WITH NOTES FROM PRINCE EDWARD AND GOUGH ISLANDS

By M. J. IMBER

ABSTRACT

In 1978 at Antipodes Islands, breeding was confirmed and distribution of breeding sites was investigated for Snares Cape Pigeons *(Daption capense australe)*, Subantarctic Fairy Prions *(Pachyptila turtur subantarctica)*, Soft-plumaged Petrels *(Pterodroma mollis mollis)*, Subantarctic Little Shearwaters *(Puffinus assimilis elegans)* and Grey-backed Storm Petrels *(Garrodia nereis)*. Breeding seasons, habits and habitats at Antipodes Islands of petrels not exceeding White-chinned Petrels *(Procellaria aequinoctialis)* in size are described. Notes are included from Prince Edward and Gough Islands on some of these species studied in 1979.

INTRODUCTION

The Bounty - Antipodes - Auckland - Snares Islands (BAAS) Expedition of 1 November to 8 December 1978 was sponsored by the New Zealand Department of Lands and Survey and the New Zealand Wildlife Service, and supported and serviced by the Royal New Zealand Navy through its frigate HMNZS *Waikato*. From 20 November to 6 December I was on Antipodes Islands (49°41'S, 178°48'E), studying the breeding Hydrobatidae, Pelecanoididae and Procellariidae, except Northern Giant Petrels *(Macronectes halli)*. Whereas the University of Canterbury Expedition had worked only on the main island from 28 January to 12 March 1969 (Warham & Bell 1979), the BAAS Expedition took place earlier in the breeding season of many species, had two boats for visiting neighbouring islets and for coastal surveys, and undertook more subterranean investigations.

In 1979, I took part in the expeditions to Prince Edward Island, from 12 to 16 September, and to Gough Island, from 30 October to 12 November, by the Percy Fitzpatrick Institute of African Ornithology, University of Cape Town. Some results of these expeditions are in press (Berruti *et al.*, Williams & Imber). Information that I present here relates to matters particularly relevant to observations on Antipodes Islands.

Of the three islands Prince Edward is the coldest, Gough the wettest and Antipodes probably the driest because of its low altitude. Vegetation is influenced accordingly: Prince Edward has sparse oceanic tundra vegetation; ferns predominate on the lowlands of Gough and

tussock grassland on Antipodes. Antipodes and Gough have a shrub each: *Coprosma* on Antipodes grows to 2-3 m, *Phylica* on Gough grows to 4-5 m and is a prominent feature of the lowlands. Tundra vegetation occurs on Antipodes above about 300 m and on Gough above 500 m. The avifaunas of the three islands are likely to vary according to their different oceanographic and geographic positions and geological ages (Table 1).

METHODS

As most of the breeding petrels of Antipodes Islands are nocturnal in their visits to land (except Cape Pigeons, Northern Giant Petrels, Fairy Prions, and some White-chinned and Grey Petrels), our daytime observations concentrated on skua-killed remains and on burrow and nest surveys. We used hand-held spotlights at night to identify and bring down petrels flying overhead. Many were also brought down by outside lights at our base camp. On Antipodes Island I prepared

TABLE 1 — A comparison of geographic, oceanographic and geological features of Antipodes, Prince Edward and Gough Islands

Islands	Antipodes	Prince Edward	Gough
Ocean	South Pacific	Indian	South Atlantic
Co-ordinates	49° 41'S, 178° 48'E	46° 38'S, 38°E	40° 20'S, 9° 55'W
Area (ha)	2025	4400	6500
Altitude (m)	404	672	910
Islets[a]	7[b]	nil	c. 13
Distance south of STC[c] (km)	600	c. 500	0-300
Distance north of AC[d]	1000	c. 200	1000
Origin	volcanic	volcanic	volcanic
Approx. age (my) [e]	less than 1	up to 0.3	almost 5

a   Large enough to have potential for nesting by birds

b   Bollons Island covers about 57 ha

c   Subtropical convergence

d   Antarctic convergence

e   million years

study burrows for observing breeding habits of Soft-plumaged and White-chinned Petrels by digging a shaft to the side of the nest chamber and fitting a peat lid. No desertions were noted.   ı

A clinker-built boat was used at Antipodes Islands for surveying petrels nesting in the coastal cliffs, and the main island was circum-navigated on 29 November 1978. An inflatable boat was also used to visit the lesser islands. We visited Bollons, Archway and inner Windward Islands. Leeward, Orde Lees and the outer pair of Wind-ward Islands are inaccessible, except by helicopter and, perhaps, to experienced rock-climbers.

RESULTS AND DISCUSSION

SNARES CAPE PIGEON *Daption capense australe*

Oliver's (1955) report that Cape Pigeons breed " in large numbers on Leeward Island " is not supported by a reference and seems to have been conjectural and exaggerated. Though suspected, breeding was not confirmed by Warham & Bell (1979). First, R. Wahrlich found an isolated nest, with an egg being incubated in late November, on a ledge behind the Anchorage Bay penguin colony. The main breeding concentration was on the north side of Archway I., where we counted about 80 occupied sites on 29 November. On the same day, while circumnavigating the main island, we mapped breeding or prospecting sites (Fig. 1). The total breeding population was probably c.300 pairs, if breeding was taking place at most sites occupied. Most sites were in niches in cliffs but some were in sheltered spots near the top of islets and stacks. Birds were regularly seen in groups on the sea where, as they were often pecking at the surface, they were probably feeding on zooplankton.

SUBANTARCTIC FAIRY PRION *Pachyptila turtur subantarctica*

I agree on ecological grounds (1981) with Harper (1980) in recognising the validity of this subspecies, described by Oliver (1955) from these islands. Breeding at Antipodes Islands, presumed by Oliver, required confirmation (Warham & Bell).

We saw Fairy Prions commonly flying around the coasts of Antipodes Island at any time of day. They were concentrating around suitable nesting habitat (rock falls and caves eroded by the sea), which we mapped during the Cape Pigeon survey (Fig. 1). Incubat-ing birds were seen in a cliff-base rock pile in Anchorage Bay and in a cave at the head of an inlet on the west coast just south of North Cape. During our circumnavigation I landed and entered this cave. Its floor comprised large sea-worn boulders, and the prions were nesting among these, at risk of flooding by an exceptionally high tide. I withdrew one bird and its egg, precariously placed on a little debris lodged between two boulders. Its chattering protests evoked responses from several neighbours, by which I estimated there were up to 20 nests in the cave.
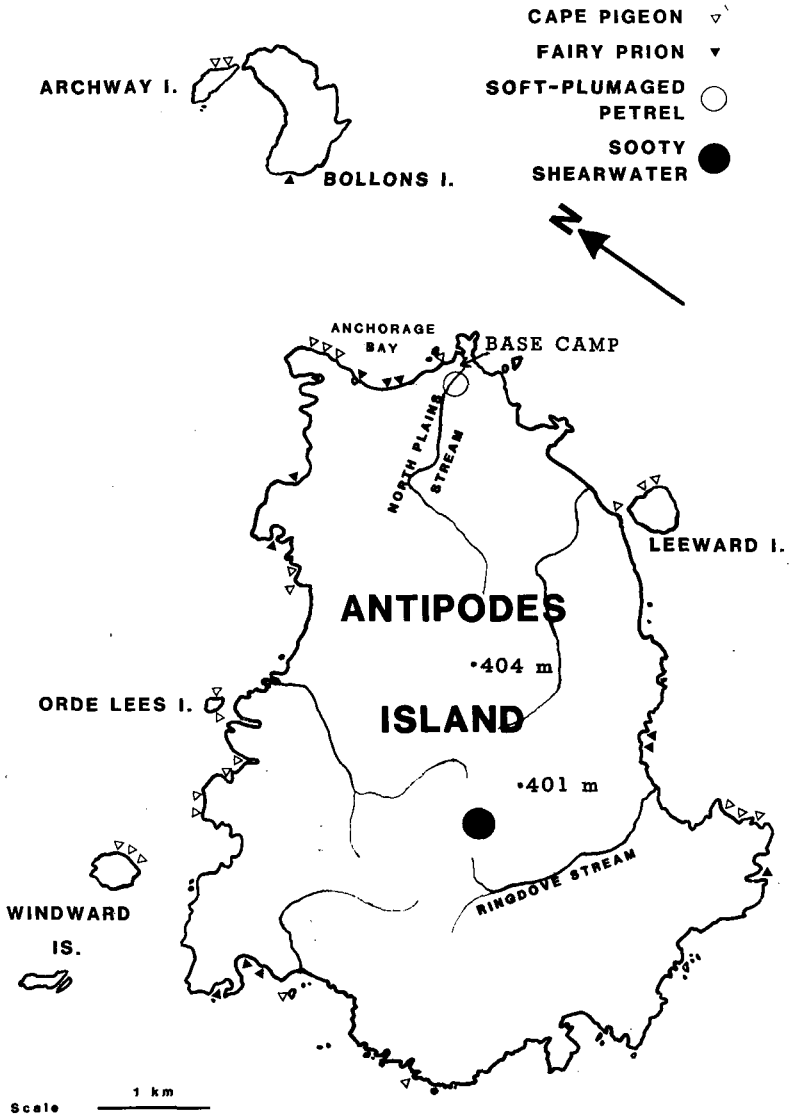
FIGURE 1 — Antipodes Islands and the breeding sites of some less abundant petrels

Prions flying around these nesting sites by day seemed to be non-breeders, as only rarely was one seen to land and scramble quickly for cover. One pair of Southern Skuas *(Stercorarius skua lonnbergi)* had their territory near the colony in Anchorage Bay and were taking some but most prion colonies seemed secure from skuas. Prions were not important in the diet of skuas here, mainly because prions were scarce and inaccessible, and this partly explains the low breeding success of skuas and their attacks on larger petrels (Moors 1980).

Prions were captured by light at night at base camp and in Ringdove Valley, two being collected for the National Museum. These and about 20 skulls discarded or regurgitated by skuas I identified as Subantarctic Fairy Prions by their small bills with moderate unguis set well forward of the nostrils, and their pale faces. One regurgitated two Pteropoda and two small fish, *Maurolicus muelleri.*

At Prince Edward Island on 16 September a few prions were seen flying around the mouth of a coastal cave. One came close enough for the small bill and wide dark tail-tip to be seen, but they might have been either *P. turtur* or *P. crassirostris.* However, only the Subantarctic Fairy Prion is known from nearby Marion Island, where it breeds in the coastal zone in much greater numbers than previously realised (Berruti 1981). As elsewhere, its strictly coastal nesting and rather brief period of diurnal activity inshore (September-December) have disguised its status.

WHITE-HEADED PETREL *Pterodroma lessonii*

This is one of the most abundant breeding petrels at Antipodes Islands, but our surveys showed that very few breed on the lesser islands visited (Bollons, Archway, inner Windward). It is the main prey of Southern Skuas on the main island (Moors 1980). The expedition took place largely during the prelaying absence of breeders, and so I did not prepare any study burrows. Burrows examined casually, by probing from the entrance or accidentally broken into, had prepared nests but no eggs and usually no birds. Cephalopods and mysids were food items I recorded.

SOFT-PLUMAGED PETREL *Pterodroma mollis mollis*

This species was first discovered in the South Pacific Ocean during the previous expedition (Warham & Bell). Breeding was not then confirmed, and so this was one of my main objectives. Brooke *et al.* (1981) have separated the southern populations of this species into two subspecies, the typical one breeding only at Gough I. and in the Tristan da Cunha group, and *P. m. dubia* reportedly breeding at Marion, Prince Edward, Crozet and Antipodes Islands. However, the Antipodes birds are the pale-mantled *mollis*, not the darker form *dubia.* This is evident in the photograph in Warham & Bell and I found no variation in plumage of the 22 I handled, of which I banded 20.

The burrows were at the head of the small valley in which base camp is situated (Fig. 1). There the vegetation attains 2 m height in places, comprising mainly *Polystichum* fern and *Poa* tussocks with patches of *Coprosma antipoda*. Burrows were dug into peat so porous that I could dig observation holes merely by forcing my hand through it, and they were mainly 1-1.5 m long, curving and quite dry. Soft-plumaged Petrels were the main species breeding in this area, although there were some White-headed Petrels, few Grey Petrels and some White-chinned Petrels on the periphery. This is where the previous expedition caught these petrels but did not find their burrows (J. Warham, pers. comm.).

Because of the density of the vegetation there I was unable to census the burrows but, comparing the area in which I worked (which held 14 burrows) with the total area over which Soft-plumaged Petrels were active at night, I estimated a maximum of 50-100 burrows in the colony. All burrows seen were in use and one of my 11 study burrows was being newly dug. Two of the nine prebreeders caught on the night of 4 December had earth on their bills, showing that they had been digging. All these signs gave me the impression that, although small, the colony was expanding.

Because the colony is in tall vegetation, these petrels are almost immune from Southern Skuas. However, three recent corpses were found in a skua territory on North Plains immediately adjacent to this valley. Warham & Bell found no corpses. Either skuas had gained access along our track from base camp to North Plains, or the colony was expanding and some prebreeders were prospecting beyond the safety of the valley. We found no evidence of Soft-plumaged Petrels anywhere else, through remains of skua kills, calls heard at night, or burrows of appropriate size.

I inspected study burrows daily between 22 November and 5 December, except on the 26th, 29th, 2nd and 3rd. All but two had recently made copious nests of fern fragments and grass. I covered entrances with fern twigs and found that five nests were not visited during the period of study, two were visited by the apparent male for two and three consecutive days, and pairs visited the other two nests. Each pair spent at least two consecutive days in the burrow. The last inspection, on 5 December, revealed no eggs. These observations indicate that most pairs were on their prelaying absence and that laying might have begun soon after our departure. I have observed (1976) a similar pattern of behaviour in Grey-faced Petrels *(P. macroptera gouldi)* where, after mating, both depart but the male returns alone for a few days before both are continuously absent until laying. As Soft-plumaged Petrels are smaller, and summer breeders, their prelaying absence is likely to be shorter than the 7-9 weeks of Grey-faced Petrels but probably as long as the 4-5 weeks of Cook's Petrels *(P. cookii)* (pers. obs.). Thus some females, such as the one I observed on the nest with her mate on 1 December,

probably do not lay until early January. Main laying in December was also implied by Despin *et al.* (1972) for Soft-plumaged Petrels on East I., Crozet Islands.

All petrels handled were in the final stages of moult. Most had to complete moult of the upper wing-coverts and had the outer-most primary not fully grown. One showed tail moult and another still had the old outermost primary. Thus, moult takes place just before rather than just after the breeding season, as it does also in White-headed Petrels (Warham 1967; pers. obs.). All had downy incubation patches, which is consistent with absence of eggs in the study nests.

Most birds found in burrows, all presumed to be breeders, were weighed and found to be heavier than those weighed by Warham & Bell, which I think were mainly prebreeders. Thus three presumed males weighed 288, 322 and 327 g and a presumed female 305 g, sexed by the criteria I established for Grey-faced Petrels (1971).

At Prince Edward Island in mid-September Soft-plumaged Petrels had just begun re-occupying burrows after their winter absence. Courtship activity was in full progress at Gough Island in early November.

GREY PETREL *Procellaria cinerea*

The breeding season of this winter breeder was nearly finished when I arrived on Antipodes Island. Many large burrows were empty but infested with fleas, and so Grey Petrel fledglings had presumably vacated them recently. We last saw an incoming adult flying among the White-chinned Petrels on the evening of 21 November. A fully fledged chick was found in a burrow on top of Bollons Island on 29 November. A freshly killed chick with downy tips to many of its wing coverts, which was found in Ringdove Valley on 1 December, probably would not have departed until about 10 December. Most chicks leave in late October and early November (Warham & Bell).

At Gough Island, where the breeding population is sparsely scattered about the uplands above 400 m, I saw no live Grey Petrels during early November, but remains of a few skua-killed fledglings showed that departures were in progress. Swales (1965) reported a similar chronology of breeding activities at Gough Island to that at Antipodes Islands, including a late fledgling on 10 December.

At Prince Edward Island on 14 September, we saw a pair of skuas molesting a fully fledged Grey Petrel which presumably had been preparing to leave by day. We intervened and, when launched, the chick flew strongly out to sea. Adults were still arriving at dusk to feed younger chicks during our visit.

At Tristan da Cunha, Elliott (1957) noted that laying extended from early in April to well into June. He saw a fully fledged chick on 15 September which had hatched before 6 June. At Kerguelen, Paulian

Little Shearwaters were very common between Bounty Islands and Antipodes Islands on 20 November (Jenkins 1981). Although it seemed that a considerable breeding colony awaited discovery, we found no evidence of breeding on Antipodes Island. By a pond on North Plains, frequented by non-breeding skuas, I found regurgitated skulls, but nowhere else on the main island did we see remains. Their occurrence over base camp at night was inconsistent, and only on our last night ashore, when thick mist descended, were many seen. However, we found that Bollons, Archway and inner Windward Islands were almost monopolised by dense colonies of this shearwater. There were few other burrowing petrels, except Grey Petrels on top of Bollons Island. An indication of the extent to which Little Shearwaters predominated is given by skua-killed remains: 94% of 202 recent petrel remains from islets were this species, the others being Grey Petrels and a Black-bellied Storm Petrel.

On Bollons Island on 29 November I could reach many nests from the entrance, burrows being often 0.5-1.0 m long, rarely up to about 2 m. All were quite dry, largely because the island is steep. I found chicks in about half the burrows explored and withdrew eight for examination. The youngest, about 3 days old, was still guarded by a parent. Most were much larger and downy without sign of feathers. The oldest showed growing wing quills. Thus, hatching had occurred between 20 October and 26 November. I assumed a fledging period of 70-75 days and an incubation period of about 52 days for this species (Glauert 1946) in deducing that laying had occurred between the end of August and early October, probably with a peak around 10-15 September, and that departures would take place between the end of December and mid-February.

I examined the five specimens in the National Museum collected on the night of 27 February 1969 by the previous expedition (Warham & Bell). They are neither recently fledged young nor adults that had just reared young (which would have been in worn plumage or in moult) but are recently moulted adults (one with short outer primary) and their fine bills indicate youthfulness. Glauert (1946) and Jouanin (1964) observed the return of birds to the breeding grounds within one to two months of the departure of fledglings, which explains the captures reported by Warham & Bell. It appears that prebreeders and possibly failed breeders return to Antipodes Islands within one month of departure of the last of the young, in what Jouanin (1964) has termed protogamic behaviour.

The breeding population at Antipodes Islands must amount to some multiple of 10^5 pairs and is therefore the largest population of this species in the New Zealand region. At Auckland Islands, Little Shearwaters frequent the sheltered fjords during winter months (the late R. A. Falla, pers. comm.). As they were thought to be winter breeders these occurrences were considered to indicate local breeding (Falla 1965) but, despite considerable biological research

at Auckland Islands in the last decade, no such evidence has been found. These winter sightings are more likely to have been of visitors from Antipodes Islands, possibly exploiting a temporary food such as sprats *(Sprattus antipodum)*, which occur off Auckland Islands and spawn mainly in winter (Baker 1973).

Jehl (1973) compared specimens of Subantarctic Little Shearwaters collected in the eastern South Pacific off Chile in June 1970 (the first reported from near the west coast of South America) with specimens of known origin. He considered them most like specimens collected near Antipodes Islands. Although there may be breeding colonies off the Chilean coast, there may also be a partial migration of Antipodes birds across the South Pacific. Solander's unpublished *Procellaria munda* was a Little Shearwater collected on Cook's first voyage further west of Chile near 48°S, 93°W (Bourne 1959).

Little Shearwaters have not been seen ashore alive at Marion or Prince Edward Islands, but a flock of over 100 was close to the latter in November 1977 and a skua-killed corpse was found ashore (Williams & Burger 1978).

At Gough Island the breeding season of this species had not been determined, although Swales (1965) considered it to be in the winter. The only evidence I found of Little Shearwaters around the Base at Transvaal Bay was a few skua-killed corpses. As Swales reported them abundant in the Glen, over 3 km to the north-west, an opportunity to search for burrows came when W. R. P. Bourne and I spent 8-11 November there. I examined burrows in a fern-clad slope opposite the old Base, in wet peaty soil. After hours of delving I had checked about 12 burrows of Broad-billed Prions *(Pachyptila vittata)*, all empty but for remains of eggs and three small dead chicks; four of Diving Petrels *(Pelecanoides urinatrix)*, whose nests I did not try to reach; two of Soft-plumaged Petrels, empty with nests; and four of Atlantic Petrels *(Pterodroma incerta)*, one with a live chick, one with a dead chick and two empty. Later, however, I found three Little Shearwater burrows. As at Antipodes Islands, they were quite short (0.4-1.0 m long) and in dry situations, one beside a volcanic dyke and two under *Spartina arundinacea* (which grows 2-3 m high in the form of bamboo-like tussocks). All contained incubating birds and one egg was pipped; so hatching would have occurred from 10 November. Thus, the breeding season is in spring at both Antipodes and Gough Islands, and it was possibly later at Gough in 1979 than at Antipodes in 1978. I did not measure the eggs.

It is difficult to understand the reported absence of Little Shearwaters at the Glen in November-December 1955 (Swales 1965) in view of their breeding season and conspicuousness at night in early November 1979. The increasing frequency of sightings reported by Swales from 10 January was almost certainly caused by departing fledglings and, especially in early April, by protogamic behaviour.

The stomach contents of a chick from Bollons I. comprised euphausiids and small squids (juveniles of *Nototodarus* sp.). An adult's stomach from Gough Island also contained remains of juveniles of the common local ommastrephid squid (*Todarodes* sp.).

GREY-BACKED STORM PETREL *Garrodia nereis*

As breeding at Antipodes Islands had not been confirmed, I spent several hours on 24 November searching for nests in tall coastal tussock near base camp but found only three then: one with a bird incubating (egg 31.6 x 23.3 mm, 9.0 g) was against a rock outcrop overhung by grass, and the other two were among the mostly dead stalks of *Poa litorosa* tussock bases and were empty. On the night of 25 November a female about to lay, weighing 41 g, was caught. P. J. Moors found shell of an egg eaten by mice *(Mus musculus)*. These storm petrels were common at night around base camp but less numerous than Black-bellied Storm Petrels in Ringdove Valley. We found a corpse on Bollons I. I heard calling (a monotonous regularly repeated chirping) from a few nest sites, one such bird having a nest 0.5 m above the ground against a *Polystichum* fern trunk in a pile of vegetation cleared from the site of the new hut. The one stomach I examined contained remains of young barnacles.

Breeding is likely on Prince Edward Island because we observed a bird calling by a *Carex* tussock. At Gough Island possibly these storm petrels breed on the cliffs or on islets and stacks, about 13 of which seem sufficiently vegetated. Clancey (1981) recorded a female about to lay taken at Gough Base on 28 October. The long wings and tails he reported for five females are due entirely to sexual dimorphism in wing and tail dimensions (my unpubl. data).

BLACK-BELLIED STORM PETREL *Fregetta tropica*

Breeding at Antipodes Islands had not been confirmed (Warham & Bell). We saw these petrels regularly at base camp at night but found no evidence of breeding in its vicinity. However, in Ringdove Valley on 1-2 December I found them to be numerous and discovered burrows in stream banks and in hummocky peaty ground. Some adults had been killed there by skuas. On 1 December one landed near me soon after dusk and entered a burrow going deep into a bank. To judge by the abundant filoplumes on its head and neck it was a male, and its incubation patch was partly bare. I heard no calls. On reflection I regret not having determined the contents of nests in the burrows in Ringdove Valley. We found remains of one bird on Bollons Island.

Black-bellied Storm Petrels had been rarely seen at Marion and Prince Edward Islands until 1974-1977, when several visits were made to the latter (Williams & Burger 1978), and evidence of breeding was not found until our visit to Prince Edward Island (Berruti *et al.* 1981). On our first night ashore, 12 September, several were

seen and heard near our camp at Cave Bay. The call was a far-carrying whistle (Beck & Brown 1971) uttered from the burrow entrance or nest. The whistle of one bird, sitting at the entrance to a burrow running into a bank, was of such power and pitch that it was physically painful to my ears 5 m away. On 15 September, while surveying burrows on the south-east slope, I heard a repeated whistle at midday coming from among jumbled rocks of a sparsely vegetated, geologically recent lava flow. This flow, spreading south-east from Wolkberg Peak, covers several hundred hectares, providing an extensive area of nesting habitat for this petrel. Although we could not find the ventriloquist, we found a mummified fledgling in an old nest and several nests newly prepared. These were under basalt blocks and in rock piles. Mosses had been plucked to make the nests. That nests were common in the small area searched suggests a very large breeding population there.

It appears that these storm petrels returned to Prince Edward Island at the beginning of September. Beck & Brown (1971) found that about 5 weeks elapsed between the return and the beginning of laying at Signy Island, and such an interval seems typical for storm petrels (pers. obs.). Thus, laying should begin on Prince Edward Island about mid-October, two months earlier than recorded for this species.

Little is known of the breeding season. Beck & Brown studied a small population (c.200 pairs) south of the Antarctic convergence where laying began after mid-December. At colonies in the sub-antarctic zone (Prince Edward, Crozet, Auckland and Antipodes Islands) breeding might be earlier but the information amounts to two eggs found on 1 February at Auckland Islands and considered recently laid (Oliver 1955). Perhaps these were late layings because the span of laying dates in storm petrels, other than those breeding at high latitudes, is usually protracted: about 2 months in White-faced Storm Petrels *(Pelagodroma marina)* (Richdale 1943, pers. obs.) and over 3 months in Grey-backed Storm Petrels (pers. obs.). Possibly laying extends from mid-October to mid-January at Black-bellied Storm Petrel colonies in the subantarctic zone. This needs to be investigated.

The absence of whistling on Antipodes Island in late November and early December may be significant. The whistle had been heard in early November 1950 (Warham & Bell). The call of the Grey-backed Storm Petrel is analogous to that of the Black-bellied Storm Petrel in being an advertisement of availability for mating (pers. obs.). Furthermore, in the former, calling seems restricted to the courtship period of pairs the females of which lay that season (pers. obs.). If Black-bellied Storm Petrels behave similarly, absence of whistling could indicate that the courtship period of breeders had finished by the end of November.

Bourne (1962), Watson (1975) and Jouanin & Mougin (1979) recorded Gough Island as the breeding place of a white-bellied race,

F. t. melanoleuca, of the Black-bellied Storm Petrel. No nest of *Fregetta* has been found there, but Swales (1965) reported an egg laid in captivity by what he identified as a White-bellied Storm Petrel *(F. grallaria).*

At Gough Island I saw no *Fregetta,* dead or alive, until we ascended to Gony Dale (500 m a.s.l.) to survey the Procellariiformes breeding high up. On 6 November, in little more than an hour of darkness between dusk and moon-rise, we heard at least five storm petrels whistling near our camp in upper Gony Dale. The whistle was similar to that heard on Prince Edward Island and the ventriloquism foiled our attempts to catch more than one bird. It had an entirely white abdomen, prominent white edgings to the mantle feathers, showed no moult, and had a downy incubation patch. Measurements were bill 14.4 mm, wing 163, tail 78, tarsus 39.8, and mid-toe plus claw 24.5. Next day I searched the slopes for nest sites but found none. Most of the terrain was waterlogged peat, and the most likely places for storm petrels' nests were isolated rock piles, but I found no evidence of nest-making at those I inspected. The storm petrel we caught, and another seen, were both on marshy ground far from potential nesting habitat. On the night of 7 November, which was cool and windy, none was heard in Gony Dale and we spent no further nights up there.

Probably these storm petrels were just returning to breed. Clancey (1981) reported one returning on 31 October, and Swales (1965) reported an egg laid on 12 January. The breeding season may thus be much later than that of indisputable Black-bellied Storm Petrels in the subantarctic zone.

The measurements of the bird we caught correspond closely with those reported by Clancey (1981) (1 bird) and by Murphy (1936) (7 birds from the Tristan da Cunha group). All seem correctly identified as White-bellied Storm Petrels. The key used by Oliver (1955) to separate *F. tropica* and *F. grallaria* was based on mid-toe length: mid-toe longer than outer toes in *tropica;* toes subequal in *grallaria.* In this respect also, our Gough Island bird seems identifiable as *grallaria.* Those 24 measured by Swales had slightly longer mid-toes plus claws (mean of 27.2 mm) but most of his may have been non-breeders with unworn claws.

SUBANTARCTIC DIVING PETREL *Pelecanoides urinatrix exsul*

This breeds on Antipodes Island but we found no evidence that it nests on the lesser islands. The burrows are concentrated along the coast and especially above sea cliffs. In this zone I found a bird incubating a soiled egg on 21 November.

Scattered burrows also occur far inland, and I removed a lone bird from one of these and confirmed its identity. On both Prince Edward and Gough Islands it was breeding commonly near the coast. Clancey (1981) considered that this is the subspecies breeding on Gough Island and that *dacunhae* cannot be maintained.

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SHORT NOTE

DUCK REMOVING EGG FROM NEST

On 28 September at 9 a.m., as I was driving along Benmorven Road, a country road 4½ km from Blenheim, I saw a Mallard *(Anas platyrhynchos)* walk across the road in front of the car carrying an egg. Its lower mandible was pushed into a hole in the side of the egg, enabling the duck to carry it. The duck dropped the egg in the long grass at the roadside, pecking at it before walking back around the front of the car and settling under a small open gorse bush in long grass on the other side of the road. The bird flushed into a narrow open drain close by, revealing a nest with 10 unhatched eggs.

Inspecting the still warm egg removed by the duck, I found that part of the shell had broken away and part of the inner membrane was stained, suggesting that a piece of eggshell had been missing for some time. A tear on the inner lining revealed an actively moving duckling. The duckling was fully formed but still a few days away from hatching, judging by the size of the yolk sac, and the egg tooth was not fully formed.

Perhaps the Mallard hen had removed the egg because the collapsed portion of the egg was irritating her while incubating or made the eggs hard to roll.

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BIOLOGY OF THE BULLER'S SHEARWATER
(Puffinus bulleri)
AT THE POOR KNIGHTS ISLANDS, NEW ZEALAND

By PETER C. HARPER

ABSTRACT

From 1963 to 1981 data were collected on the breeding of the Buller's Shearwater. The world population, roughly 2.5 million birds, occupies 7 of the 12 islands, islets, and stacks of the Poor Knights Islands (35°30'S 174°44'E).

Buller's Shearwaters return from their 4.5 month trans-equatorial migration on about 10 September. Numbers build up rapidly with breeding birds digging burrows averaging 1.01 ± 0.2 m in length. Caverns, caves, and Maori stone walls also serve as nest sites.

Nest refurbishing is complete by about 26 October, when copulation occurs. The prelaying exodus follows about 32 h later, with most birds absent from the islands' vicinity for about 30 days until 25 November.

Eggs appear from 26 to 30 November. Females without nests lay eggs on the ground until 3 December; these eggs are eaten by tuataras and small lizards. Average dimensions of 74 eggs were 65.44 ± 0.29 x 42.96 ± 0.22 mm; and average weight of 27 fresh eggs 66.76 ± 0.85 g. Surface eggs are narrower than burrow eggs.

The incubation period is c. 51 days with both sexes sharing duties. Four nights is the average shift; females sit the first night and following day. Hatching occurs about 19 January; most fledglings leave the islands in early May.

Most of the few adult *bulleri* that die on the breeding grounds are ensnared in tree saplings.

Numbers on Aorangi have expanded rapidly from c. 100 pairs in 1938 to about 200 000 pairs in 1981. *P. bulleri* is an aggressive coloniser, displacing gadfly petrels and smaller shear-waters for nesting space, and may soon be colonising the Three Kings and other nearby islands.

INTRODUCTION

The Buller's Shearwater is a subtropical surface-feeder that breeds only on the Poor Knights Islands off the east coast of northern New Zealand. It is distinctive for the brown and grey pattern of its upperparts, its all-white underparts, slender body proportions, relatively broad wings, and long wedge-shaped tail (Harper & Kinsky 1978: Fig. 13 & Plate 13). Its nearest living relative is the Wedge-tailed

Shearwater *(Puffinus pacificus)* of the subtropical and tropical Pacific and Indian Oceans. Both these birds once comprised the subgenus *Thyellodroma* of Stejneger, which Stejneger distinguished from subgenus *Puffinus* because of their long cuneate tails — nearly half the length of the wing (Murphy 1951). With a wingspan of just under a metre (995 mm) and a total body length of about 476 mm, a Buller's Shearwater in good condition weighs about 412 g — about half that of the similarly sized pursuit-plunging Sooty Shearwater *(Puffinus griseus).*

      The Buller's Shearwater was discovered in October 1884 when Walter L. Buller found a storm-tossed female on Waikanae Beach; in 1888 Salvin formally described the bird as *Puffinus bulleri* in honour of its finder.

      Its breeding grounds remained unknown for 30 more years. Six further specimens were recorded in New Zealand, and 16 were shot by collectors off Point Pinos on the coast of California (Loomis 1918). The bird was better known in California than in New Zealand until its breeding place was found in December 1915 by William Fraser, a Whangarei Harbour Board engineer whose interests included visiting offshore islands. It was Fraser who rowed R. A. Falla ashore at the Poor Knights Islands in December 1923, and Falla's paper recording the discovery of its nesting place appeared in *Emu* in 1924.

      Although the Buller's Shearwater is now well known in New Zealand and it is familiar overseas as the New Zealand Shearwater or the Grey-backed Shearwater, its breeding biology and ecology at the Poor Knights are very poorly known. As it is an endemic species confined to this small island group, concern has been expressed in recent years for its welfare; the purpose of this paper is to bring together what is known about the bird and to discuss its status.

METHODS

      In 14 visits totalling 189 days on Aorangi between 1963 and 1981 to study Fairy Prions *(Pachyptila turtur)* (see Harper 1976) I have collected anecdotal notes on *bulleri.* I foresee the greatest problem in making a detailed study of Buller's Shearwaters is that they readily desert nests. Even when I took great care with nest-observation covers and periodic monitoring of nests, I found that incubating birds would leave nests and not return for 4-5 days. They are acutely sensitive to any disturbance whatsoever.

      Birds were banded with monel or stainless steel bands from the Banding Office, Wildlife Service, Department of Internal Affairs. Field measurements were made with 150 mm stainless vernier calipers, a 1-metre stainless folding rule, and 500 g ($\pm$ 2 g) or 1000 g ($\pm$ 2 g) Pesola spring balances. Eggs were weighed with a smaller 100 g ($\pm$ 1 g) Pesola balance. Regurgitations were preserved in 70% ethyl alcohol for further analysis.

Burrows were measured and checked for occupancy with a Rabone Chesterman Lockflex flexible spring tape or a 6 m Evans Tru-Lok tape. If you insert your left arm into a burrow until you encounter a bend in the burrow, you can feed in the stiff yet flexible tape with the right hand and guide it around the corner with the left-hand fingers to the end of the burrow. This is a simple way of measuring long burrows. You can detect the softness of a sitting bird with the tape and also hear it rustling its feathers. If you rattle the tape, an adult bird leaves its nest and scuffles to the burrow entrance, where you can capture it. This technique works well with some shearwaters, with prions, and with diving petrels such as *Pelecanoides gecrgicus,* which tunnel 1.5 m deep into compacted sand dunes on Codfish Island.

I assessed rates of population increase by counting *bulleri* burrows in prion study areas, recording the takeover of other petrels' burrows by *bulleri;* by noting new burrows appearing in places previously having no burrows, and by general observations. From all this information I made estimates in 1981 of the population for Aorangi and the total *bulleri* population for the Poor Knights.

HISTORY

The Poor Knights Islands are a Nature Reserve administered by the Hauraki Gulf Maritime Park Board, Auckland. They comprise two islands of volcanic origin and a small flotilla of stacks and rocks in subtropical waters 24 km off the east coast of Northland. The highest point is Oneho Hill (218 m) on the island of Aorangi. Regenerating coastal forest covers all but the steepest precipices. For botanical notes see Cockayne (1906) and Oliver (1925).

Before 1823 both the larger island, Tawhiti Rahi (132 ha) and Aorangi (68 ha) were occupied by some 300 Maoris, whose fortifications were visible to Captain James Cook when he discovered the islands on 26 November 1769 (Beaglehole 1955). Much of the vegetation had probably been removed at this time for cultivation of vegetables and fortifications (Oliver 1925, Falla, pers. comm. 1973). Pigs were later brought to Aorangi by its Maori residents and kept secure as food and barter. Also used for barter, and considered more appetising than the " northern muttonbirds " *(Pterodroma macroptera),* was the Buller's Shearwater. In a letter to W. R. B. Oliver dated 11 July 1955, William Fraser wrote, " Rako is the Maori name of Puffinus Bulleri, and my old Ngatiwai informants of 40 to 50 years ago on this coast would tell me that their relations of the old time on the Poor Knights made a trade with the mainlanders in preserved young rako, as this species of mutton bird was in greater demand than the more common kind, and that the Maori protected the nesting places and the parent birds."

In December 1823, while the men and their chief, Tatua, were absent, the islands' inhabitants were massacred (see Fraser 1925).

The rest of the Maoris left permanently, declaring the islands tapu, or forbidden. Thereafter the pigs flourished: they stripped Aorangi bare of seedlings and ate everything palatable within reach. Petrels were rooted out of their burrows and eaten (Falla 1924, Oliver 1935). Falla found remains of *bulleri* and Fairy Prions, all "victims of the pigs' depredations" and commented that "During several hours' stay on this island no living Petrels of any kind were found, and all the burrows examined were empty." However, on Tawhiti Rahi, only 440 m away, "rako" flourished free from pig predation.

The last of the feral pigs was shot on Aorangi in 1936 and soon afterwards a low mixed forest regenerated and the seabirds re-colonised. In 1938 G. A. Buddle and C. A. Fleming found a colony of c. 100 burrows of *bulleri* "on a gently-sloping earthy shelf situated at the foot of a steep rocky face and terminating in a high cliff dropping sheer to the sea 200 feet below . . . the area at that time was shared with Prions in about equal numbers. We did not locate any other breeding areas and ascribed the presence of this colony to the fact that the ledge had probably been inaccessible to the pigs." In 1940, "the size of the colony had increased considerably and the prions had been completely ousted" (Buddle 1941). Incoming bulleri were probably from neighbouring Tawhiti Rahi, where as many as half a million birds were believed to be resident (Wilson 1959).

Other petrels were also digging in. In 1940 a further four species were reported from Aorangi: the Fluttering Shearwater *(Puffinus gavia)*, Grey-faced Petrel *(Pterodroma macroptera gouldi)*, Pycroft's Petrel *(Pterodroma pycrofti)*, Diving Petrel *(Pelecanoides urinatrix)*, and White-faced Storm Petrel *(Pelagodroma marina)*. Of these, *gavia* and *macroptera* were judged in 1940 to be the most common (Wilson 1959).

Summary of previous observations

Loomis (1918) gave measurements of 15 California specimens of *bulleri* and a detailed description of the species. He noted that "The breeding places of this Southern Hemisphere species and the route by which it reaches the vicinity of Point Pinos, California, are unknown." Six years later, Falla (1924) reported its presence at the Poor Knights Islands, reviewed its status in New Zealand, and gave a few notes on its burrow habitat, nest, eggs, and behaviour about its breeding grounds. Little further information has been added since. Brief observations were made by Buddle (1942) and Kinsky & Sibson (1959), but no breeding study of the Buller's Shearwater has been attempted.

The migration route is still not known. There is no evidence to show that they accompany Sooty Shearwaters and Short-tailed Shearwaters *(Puffinus tenuirostris)* north of the equator or that they engage in any clockwise migration around the North Pacific Ocean, but observations are lacking. Jenkins (1980) discussed the presence of

bulleri in Tongan waters but believed that the birds' migration path both to and from New Zealand waters lies well east of Tonga. Kuroda (1955, 1960) reported *bulleri* from 14.5-16 °C waters near Japan, and Wohl (1975) saw nine birds in September 1974 in the northern Gulf of Alaska. Kessel & Gibson (1976) described *bulleri* as a rare visitor to south coastal Alaska from late April to September, where it appears " singly or in twos or threes; maximum count has been 17." Campbell (1971) considered *bulleri* to be a regular autumn migrant off the British Columbia coast, and Ainley (1976) stated that " They are most numerous off California from early September to early October." Because of their scarcity south of Monterey and in the eastern Pacific south of Baja California, Ainley suggested that " Birds occurring off California probably turn towards New Zealand at about the latitude of central California."

Moulting birds have been reported not only from California waters (Loomis 1918) but also from the coast of Chile. Beck's specimens collected off Valparaiso, Chile, between 24 February and 12 March 1914 were all " moulting the quills and had nesting gonads " (Murphy 1936). These non-breeding individuals summer in the usually productive waters of the Humboldt Current while the breeding population is resident in New Zealand. At the limits of their very wide Pacific distribution, Buller's Shearwaters are frequently found at boundaries between warm and cold currents in ocean temperatures 14.5-16 °C (e.g. Japan, Kuroda 1955, 1960; California, Ainley 1976; New Zealand, Jenkins 1974).

The local movement of *bulleri* about New Zealand was the subject of a most valuable contribution by John Jenkins (1974). From summer through to late April they flock in hundreds along the east coast of the South Island of New Zealand in warm tongues of surface waters close to the Subtropical Convergence (Bartle 1974; Jenkins 1974; Harper, pers. obs). Cunningham (1948) gave measurements of 21 birds cast ashore in Palliser Bay after a southerly storm in February 1947 (see Table 1). Sea surface temperatures at the Poor Knights during the breeding season of *bulleri* range from a minimum of 16.2 °C in August to a maximum of 21.5 °C recorded in February.

THE BREEDING CYCLE

Most Buller's Shearwaters are absent from New Zealand waters from late May to early September. Jenkins (1974) observed their return. He reported that on " 11 September 1967 in a position 32°40′S 176°35′E about 160 miles north of the Poor Knights . . . for over two hours from 1630 hours until after sunset we passed through a continuous stream of Buller's Shearwaters spread out in the typical migration pattern in ones and twos and groups up to about five. Birds were seen out to the limit of visibility on both sides of the vessel's track and all were seen to be heading due south. At least several thousand birds must have passed the vessel during the late afternoon."

TABLE 1 — Measurements of Buller's Shearwaters

	Mean ± S E (mm)	Range	Number
	Loomis (1918)		
Bill length	42.3 ± 0.32	40.7 - 45	15
Wing	297.2 ± 1.68	285 - 309	14
Tail	127 ± 1.34	119 - 137	15
Tarsus	49.3 ± 0.28	47.6 - 51	15
Toe	62.0 ± 0.33	58.9 - 63.7	15
Total length	475.9 ± 3.44	460 - 493	10
Wing span	995.2 ± 4.4	980 - 1016	10
	Cunningham (1948)		
Bill length	41.33 ± 0.37	38.5 - 44.5	21
Wing	284.1 ± 2.41	268 - 300	16
Tail	no data		
Tarsus	52.45 ± 0.40	49 - 56	21
Toe	66.26 ± 0.94	61 - 68.5	21
	Buddle (1941); this study		
Bill length	41.20 ± 0.29	38.3 - 44	28
Wing	287.2 ± 2.31	275 - 300	15
Tail	125.4 ± 1.30	114 - 130	15
Tarsus	50.22 ± 0.81	47 - 57.1	17
Toe	63.64 ± 0.62	60 - 70	17

In 1981 when continuous observations were made on Aorangi from mid-August to mid-December, the first four *bulleri* appeared in flight over the island on the night of 10 September and one bird was found in a burrow. Incoming birds gradually increased until 18 September, when *bulleri* were " everywhere, either investigating or refurbishing burrows " (P. Kearton, *in litt.*). Thereafter their numbers rapidly increased as burrows were reoccupied. Corroborative inform- ation from local fishermen points to a consistent *bulleri* arrival date of the second week in September. During October and November the birds spread south along the coasts of New Zealand and remain in open continental shelf waters until late April or early May (Vooren

1972, Bartle 1974, Jenkins 1974). I observed 23 flocks, each containing between 179 and 351 birds, while at sea near Akaroa Peninsula on 19 February 1982. The birds, many in wing and body moult, were feeding on small shoaling fish.

Evening arrival on Aorangi

For much of the breeding season, Buller's Shearwaters begin arriving offshore around the islands in the late afternoon. Feeding often continues close inshore, whenever the birds pick up a shoal of trevally *(Caranx georgianus)* or similar predatory fish pursuing small prey to the surface. Storms notwithstanding, the time of the first *bulleri* over the islands at nightfall is strongly correlated with the time of sunset (Harper, in prep.). Westerly gales often delay and easterlies assist the return from the feeding grounds, which by inference, apparently lie east of the Poor Knights along the continental edge.

In places where nesting colonies are concealed by tall trees, Buller's Shearwaters usually alight briefly in the canopy branches before fluttering to the ground to land with a gentle thump; and breeding birds alight with precision near their nests. With their light weight and broad wings and tail, Buller's Shearwaters are surprisingly agile at flying along the ground under the trees and can easily flutter up and over such surface obstacles as large rocks. The strongly hooked bill, long claws, and tent-like tail make *bulleri* a deft climber of trees and sheer rock walls. Travel along the ground is accomplished in the usual shearwater waddling, but when alarmed, *bulleri* make long hops and bounds.

Eggs

Most birds favour either excavating an earth burrow 0.6 to 3.2 m long (average 1.01 ± 0.2 m, n = 179) among tree roots or occupying earth-floored caverns under large slabs of rhyolitic rock. All of 59 burrows examined had a terminal chamber sufficient to accommodate two adult birds easily. Some areas on the flat top of Tawhiti Rahi that are densely honeycombed with burrows are sufficiently clear of low ground plants to allow harriers *(Circus approximans)* to hunt prey beneath the canopy of tall gnarled pohutukawa trees (Wilson 1959). Nests are also built in caves, rock crevices, and in the convenient dark gaps within Maori stone walls. Both members of a pair dig the burrows and gather material for the nest.

Nest lining varies from the few stone fragments I found in 129 sheltered rock crevices to a substantial assemblage of leafy and twig material I found in 26 of 59 earth burrows. Sources of vegetation and twigs are chiefly the nearby canopy trees: pohutukawa *(Metrosideros excelsa)*, and karo *(Pittosporum crassifolium)*.

Birds may also strip fallen branches and seedlings of kohekohe *(Dysoxylum spectabile)* and taupata *(Coprosma repens)* to get their stiff leaves. Such trees, which are used as departure points in the morning exodus and as sources of nest material, are an important

FIGURE 1 — Adult male Buller's Shearwater incubating in a large cave. Little nest material has been used.

habitat requirement for Buller's Shearwaters nesting beneath them. Nest blocking, in which birds actively kick leaves into their burrows to disguise them (Bartle 1968) or to darken them (Warham 1960) does not occur in this species or the Wedge-tailed Shearwater. The stacks to the south of the main islands have no soil. The shearwaters improvise by nesting in the open on rock ledges and in crannies protected only by small twiggy taupata shrubs and the prostrate form of ngaio, *Myoporum laetum* var. *decumbens*. Most of the eggs in such nests were found deserted on 10 December 1964, perhaps because of the warm air temperatures (noon 24 °C with light airs).

Copulation was prevalent in the colonies on the evening of 26 October (1975 & 1981). Howling and frenetic neck-nibbling by pairs on and below ground accompanied the rush to reproduction. Even a crude imitation of the cries elicited a prompt cacophonical reply, and throughout October the island reverberated with the wailing of *bulleri* until midnight, and again two hours before dawn, when the birds departed. Many pairs (82% :211 of 256 observations) remained together in their burrows for a day and a night after copulation. Birds without nests do not remain on the island during daylight hours.

After copulation the birds leave the islands in dramatic numbers. For 30 days, while the females form their eggs (the prelaying exodus), very few *bulleri* visit the islands. The exodus by all age-groups is essentially complete from both the islands and their vicinity. None was seen at sea from the launch *Matira* during our passage to Aorangi on 15 November or our return on 21 November 1977, and during their prelaying exodus in 1964, 1973, 1977 and 1981, very few birds were seen ashore. An analysis of ring structures of *bulleri* yolks (see Grau, 1976) showed that 18 days are required for yolk formation (C. R. Grau, pers. comm.). Wedge-tailed Shearwaters at Monera I., Hawaii, have an exodus of nearly all birds for a shorter period of 6-21 days before egg-laying (Schallenberger 1973).

Some 11 weeks after their spring return to the island, *bulleri* lay their eggs. Laying for burrow-holding birds begins on 26 November and is mostly completed by 30 November: 306 of 311 (98.1%) refurbished empty nests on 27 November had eggs on 30 November (years 1964, 1973, 1979). These dates agree exactly with those obtained in 1938 and 1940 by Buddle (1941). Males return to the nests at about the same time (possibly a day or two earlier) as the females.

Females without nests continue to lay eggs on the ground until about 3 December. None of 47 such eggs was incubated by day or night and all were eventually eaten by lizards. I saw three eggs being eaten by tuataras *(Sphenodon punctatus)* and one by the large gecko *Hoplodactylus duvauceli*. The crespuscular skink *Leiolopisma oliveri* has been seen feeding from cracked *bulleri* eggs on three occasions. I know of four eggs that were still intact on the ground a year after they had been laid.

FIGURE 2 — A day-old Buller's Shearwater chick in a substantial nest in a deep cavern below ground level. The sword-like leaves are from **Xeronema callistemon**, the Poor Knights lily. All the nest material has fallen into the cavern from above.

Measurements of 104 eggs from Aorangi and Tawhiti Rahi are given in Table 2. The differences between the two populations are insignificant (L.B.2 index 120.7 for Aorangi; 120.1 for Tawhiti Rahi). There is a highly significant difference ($p < 0.001$) in the width of eggs between those laid in the open, on the ground, and those laid in burrows. The lengths are barely significantly different (Table 3). The bare brood patches of 20 incubating birds measured in early January 1973 averaged 73 x 48 mm, which is 5-7 mm larger than the largest measured egg (Table 2). The egg represents about 16.4% of the net weight (with empty proventriculus) of an adult bird in good condition (taken to be about 407 g: see Table 4).

During incubation from late November to mid-January air temperatures on Aorangi are warm (noon max. shade 27 °C, noon min shade 13 °C; means 21 ° and 16 ° respectively). An embryo within a *bulleri* egg can survive 8 days without incubation in these temperatures. Absences of more than a day or two are rare, however.

If a nest and freshly laid egg are left unattended, the nest is sometimes usurped by a female without territory, and the nest then has two eggs. I recorded this on five occasions. In all five, the interloper was ejected by the owner. In three, the alien egg disappeared immediately, but in two, it was brooded under the wing for 2-7 days before disappearing.

TABLE 2 — Measurements of Buller's Shearwater eggs from Aorangi and Tawhiti Rahi

	n	Mean ± S E	Range
		· Aorangi (this study)	
Length (mm)	74	65.44 ± 0.29	59.0 - 72.3
Breadth (mm)	74	42.96 ± 0.22	40.1 - 46.1
Weight (g)*	27	66.76 ± 0.85	59.0 - 74.0
		Tawhiti Rahi	
		(Falla 1924; Hamilton unpubl. data)	
Length (mm)	30	64.32 ± 0.37	60.0 - 68.0
Breadth (mm)	30	43.22 ± 0.19	41.3 - 45.1
Weight (g)	no data		

* Eggs less than 10 days from laying

Because the birds are so easily disturbed, I did not study closely the incubation shifts of partners. Eighteen observations of five banded pairs gave a median incubation stint of 4 nights (range 4-7 nights). This is much shorter than the average of 9.4 days (n = 32 incubation stints) reported for Sooty Shearwaters at The Snares by Warham et al. (1982), who found only two shifts of less than 8 days' duration. Females incubate for the first night and the following day (n = 37). Thereafter the male takes over for the first full incubation stint. This may not be as easy as it seems. One incident highlights the problems inexperienced birds may have in incubating eggs. An unbanded male having relieved his mate on a freshly laid egg gave me the clear impression that he had no notion of what to do with it. The bird played hockey with bill and egg for 16 minutes, during which the egg made four circuits of the nest chamber. I later found the egg in a vertical position with the sleeping bird leaning against it. The next night the egg was nestled alongside the bird under its wing. Success was eventually achieved 24 hours later.

With the precision well known for migratory shearwaters, the hatching of *bulleri* occurred in mid-January (mean 19 ± 1.7 January, range 17-26; n = 86). This gives an approximate average incubation period of 51 days. This figure is probably close to the true one, but I could not follow known-aged eggs throughout the period. Wilson (1959) reported *bulleri* hatchings on 19 January 1943. He stated " As we had found on our previous trip, that the earliest egg had been late in November, this would mean about fifty days incubation, the same period as Lockley found with his Manx Shearwaters." The dates remain the same 40 years later.

Chicks

I have almost no information on the chick stage of *P. bulleri.* Falla (1934) reported that four well-grown nestlings in down taken on 24 February were " fairly uniform in size and colour of down,

TABLE 3 — Measurement differences between surface and burrow-laid eggs of Buller's Shearwaters

Where laid	n	Length ± S E	Breadth ± S E	L B^2 + S E
Surface*	33	65.93 ± 0.44	42.38 ± 0.21	118.63 ± 1.61
Burrow**	18	64.23 ± 0.71	43.78 ± 0.29	123.49 ± 1.89
P		< 0.005	<0.001	n.s.

*   all presumably laid by young birds. None hatched.

**   all hatched successfully

TABLE 4 — Evening and morning weights of 120 adult Buller's Shearwaters weighed in January 1973

(January)	No. of Weighings	Mean $\pm$ S E (g)	Range (g)
Evening Arrival			
16	30	452.0 $\pm$ 3.75	408 - 488
21	30	452.5 $\pm$ 5.24	385 - 490
Morning Weights			
19	30	406.8 $\pm$ 7.41	339 - 499
22	30	416.7 $\pm$ 5.88	380 - 480

which is a neutral grey, only slightly darker above than below." He continued, " Bill and feet are coloured as in the adult, but more fleshy and with dark parts less pigmented."

According to Falla, fledglings " leave the nests about the end of March, and by the end of April very few birds of this species are to be seen at sea." In a visit on 11-17 May 1976, I found 23 fledglings, together with three chicks still in mesoptyle down but with well-grown quills. It seems likely that most fledglings leave the islands about mid to late May (P. Sagar, pers. comm.; pers. obs.). Information is required. Fledglings have considerable dark flecking on the undertail-covert extremities, not a feature of adult birds. Chick mortality may be higher for late birds because, despite a careful search in high-density burrow areas, I found seven freshly dead fledglings but no young birds that had been dead for more than a week.

Unemployed birds

On Aorangi, a large percentage of the population is without a nest, or fails early to produce a chick; my guess is 40-50%. During the hours of darkness, unemployed birds arrive in great numbers and are both conspicuous and noisy. Their many activities include arriving at the colonies at any hour until 0200 h, exploring burrows (see Harper 1976), sitting about on the ground sleeping, gathering twigs and fallen leaves into small heaps on the ground, and forming twos and threes for howling sessions (Fig. 4). Their noise often stimulates chorusing and pair-bond behaviour between mated pairs of both *bulleri* and Fairy Prions on their nests. This interspecific stimulation is conspicuous and widespread throughout mixed colonies of prions and shearwaters. It can easily be initiated by a tape recording.

FIGURE 3 — Two unemployed birds spar at each other while seeking nesting territory. Fights by birds on the surface of the ground are rare.

When the evening's activities have subsided shortly after midnight, unemployed birds ignore or take little interest in one another. They sometimes ritualistically gape and spar at passing birds. This refractory period, which may last 2.5 h, seems so stupefying for the birds that I once saw a motionless bird (eyes open) succumb to gravity and fall sideways off a large rock to the ground. A prion can climb unharmed over a *bulleri* that is in this catatonic state.

Breeding birds on territory are very different, however. Burrows rarely have more than one entrance, and anything entering an occupied one must face the occupant's combined urges to flee and to fight. The result is immediate, noisy, and savage. I have, for example, seen a very large male tuatara (70 cm in length) rapidly reversing out of a *bulleri* burrow with the screaming occupant's beak embedded in its snout. On two occasions shearwaters have emerged from their burrows to attack us as we passed by some 2.5 m away. This heightened belligerence probably results from many invasions of privacy by unemployed birds. Away from areas of high density, birds were noticeably less aggressive.

The departure of nearly all birds for the prelaying exodus in late October is dramatic. Why do birds without burrows not take their pick of the huge number of cleaned-out and refurbished burrows thus abandoned? This does not happen, and returning females heavy with their eggs are not to my knowledge opposed in the reoccupation of their nests. The unemployed birds apparently do not return in important numbers for a night or two after the main influx of females, a seemingly neat arrangement that deserves study.

In late December, some three weeks before the chicks hatch, unemployed shearwaters begin leaving the islands. As a result, the colonies become much quieter and above-ground activity drops away. This departure of unemployed birds, which must relieve the adjacent food supplies and so improve the chick success rate, also deserves study. Where these birds go is not known.

Mortality

Mortality of adult *bulleri* on Aorangi is low. In 14 visits from 1963 to 1981 I have recorded 24 dead birds. Of these, 20 were caught by the legs or wings in saplings of mahoe *(Melicytes ramiflorus)*, one flying female with a shelled egg in her oviduct struck a boulder and died instantly, one died after failing to dislodge itself from under a boulder, and two were found dead from unknown causes. Harriers may take fledgling *bulleri* on their first journey to sea, but I have not seen a harrier press home an attack on flying *bulleri*. The limited banding records so far suggest that Buller's Shearwaters are long-lived birds.

Feeding behaviour and food

Buller's Shearwaters feed on a variety of prey by contact dipping and surface feeding. On only two of 211 observations of feeding

birds near the Poor Knights and Akaroa Peninsula have I seen birds plunge briefly below the surface.

The feeding technique of *bulleri* is precisely that described for its close relative the Wedge-tailed Shearwater by King (1974). He writes: " In contact dipping birds flew close to the surface, wings held back as if to hover, sometimes touching the surface with outstretched feet. Head and neck were plunged down several inches into the water. Forward momentum was regained by vigorous wing beats and foot paddling. Usually when a fish was caught it was eaten without interrupting flight although birds stopped on the surface occasionally, presumably to swallow heavy prey." Such behaviour is commonly used by *bulleri* flocks working areas where predatory fish have forced small sprats to the surface. On 8 January 1973, for example, a flock of 3000 *bulleri* was seen offshore from Aorangi working systematically into the wind around a maelstrom of fish, gathering small prey from the surface in the manner described above, before wheeling back in order to repeat the process. On other occasions the birds appeared not to be catching fish, but in the words of Jenkins (1974), " collecting the remains of the banquet which is being enjoyed by the biggest predatory fish."

Buller's Shearwaters also take prey by surface feeding. In light airs birds abruptly descend to alight on the water and, with their wings held half open, lunge this way and that with their long necks to capture prey. Those observed from only a metre or two away were snatching crustaceans from the water. Salps and jellyfish are also eaten.

Of 30 regurgitations from birds caught on the breeding grounds between October and January, 23 (76.6%) were composed solely of the euphausiid *Nyctiphanes australis* and the rest were a mixture of small fish flesh and euphausiids. The size class of the crustaceans was remarkably uniform (mean 12.9 mm $\pm$ 0.1 mm, range 8.9-17.1 mm; n = 5112). Regurgitations over the same period from the much smaller Fairy Prion yielded the same food in the same size range (mean 12.8 $\pm$ 0.1, range 8.9-16.3 mm; n = 733). The two species must therefore have been taking the prey abundantly available rather than being selective. At other times of year, their foods may well be quite different.

The crustaceans had been ingested just before the birds came ashore. For example, the heaviest *bulleri* at 499 g (Table 4) was caught at 0342 h on 19 January 1973. The bird's bill, head and feet were still wet with sea water, and it regurgitated 59 g of barely dead *Nyctiphanes*. This bird, like several others, was presumed to be a failed breeder visiting the islands briefly before the morning departure.

Nearly all the regurgitated euphausiids were intact. That the Buller's Shearwater's superbly adapted grasping and chopping beak should admit such small soft organisms without even dislodging their

FIGURE 4 — A trio of unemployed birds howling together. Such birds sometimes gather piles of twigs near them, a ritualistic nest-building.

eye-stalks shows how deftly the birds can retrieve small items from the water.

THE FUTURE

On the Poor Knights, *bulleri* is an aggressive coloniser. From the low hundreds in 1938 its numbers on Aorangi have risen so greatly that in 1981 their numbers were roughly 200 000 (Bartle 1968; pers. obs.). This extraordinary rate of increase has probably been largely due to immigration from Tawhiti Rahi and has been at the expense of other petrels, including Grey-faced Petrels and Fluttering Shearwaters *(Puffinus gavia)*. In late November 1940, Wilson (1959) reported from Aorangi that not only were Fairy Prions " breeding in good numbers in crevices in the rocks " but also that " The most common of the other petrels were *gavia,* a species with extraordinary raucous cries, which filled the air at night on their homecoming, and *macroptera,* mostly either ready to fly or already flown." A single pair of *macroptera* seen courting on the ground by J. A. Bartle in 1965 remained the only positive recent Aorangi record of the species until a visit by Paul Sagar and others between 30 April to 9 May 1983, when about a dozen birds were seen in aerial courtship flights or were captured on the ground in Puweto Valley. Whether these birds were visiting or are actually breeding on Aorangi is not known.

Fluttering Shearwaters also suffer. Eleven burrows of *gavia* that were near the outfall of Puweto Stream in 1964 were all occupied by *bulleri* in 1975. Six chicks of Allied Shearwater *(Puffinus assimilis)* raised by this winter-breeding species are also known to have been evicted by *bulleri* seeking territory. A dead adult Sooty Shearwater found in a burrowed area near the summit of Aorangi in November 1963 is the only recent record of *griseus* from the island. Now occupied by *bulleri* only, the site may have been used in the past by Sooty Shearwaters. A single breeding pair of *griseus* was found on Tawhiti Rahi in December 1958 by Kinsky & Sibson (1959), who believed that " the aggressiveness of *bulleri* is the reason for the scarcity of other breeding petrels on this island."

Fairy Prions have fared better than most, largely because they now nest in small crevices, bound on all sides by rock, that *bulleri* cannot get into. Prions occupying a nest with a soil wall or floor, however, run the risk of having it enlarged and their nest contents thrown out (Harper 1976). The Buller's Shearwater is thus a successful competitor for nest space on the Poor Knights Islands. Provided food does not become limiting, it may soon need more nest space, and so other islands such as the Three Kings and the Hen and Chickens may soon be visited by colonists. The effect of this on the small population of Pycroft's Petrel at Hen Island is a matter of concern.

Further studies could be made on the following topics:

1. Information on the migratory pathways of *bulleri* is very scant. The whereabouts of feeding areas important to the species, both in

New Zealand waters and beyond, needs to be known, particularly if such areas are exposed to large-scale commercial fishing or frequent oil pollution.

2.   The foods of *bulleri* are largely unknown. Shoaling fish, squid, and crustaceans are likely prey, but detailed and quantified accounts are needed of the bird's diet throughout the year. Means are available for harmlessly flushing out contents of the proventriculus.

3.   More information is needed on most aspects of breeding biology of *bulleri*, but study is not easy because incubating birds desert readily. The chick period from hatching to fledging needs study, particularly the composition and frequency of meals.

4.   A census of the breeding population of *bulleri* can probably be done on Aorangi; but on Tawhiti Rahi, the number of burrows is too great and too many would be destroyed in a full census.

Despite the well-known risks of a species breeding in only one place, the future for the Buller's Shearwater looks promising, especially if the islands continue to be free of rats.

ACKNOWLEDGEMENTS

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SHORT NOTE

PREDATION OF GOLDFINCH BY NEW ZEALAND KINGFISHER

The predation of an adult male Goldfinch *(Carduelis carduelis)* by a New Zealand Kingfisher *(Halcyon sancta)* was observed on 24 July 1981 at Pukepuke Wildlife Management Reserve.

The Kingfisher was perched on a cabbage tree overlooking a patch of beggar's ticks *(Bidens frondosa)*, where a small flock of Goldfinches was feeding. At my approach, the finches took flight, and at the same instant the Kingfisher swooped down and caught a male in flight. Death was almost instantaneous with the Goldfinch struggling and squealing for about two seconds before going limp. The Kingfisher took its prey back to the cabbage tree, where it repositioned it in its bill and then flew out of sight.

From the position of the Kingfisher's perch over the feeding finches, it was almost certainly watching them, waiting for an opportunity to take one.

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THE AFFINITIES OF THE
NEW ZEALAND PASSERINE GENUS Turnagra

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ABSTRACT

The external structure, pterylosis, myology, and osteology of *Turnagra* show that this genus belongs in the bird-of-paradise/ bowerbird assemblage and is not closely related to the Pachycephalinae. *Turnagra* appears to be the most primitive member of this assemblage, sharing similarities both with the paradisaeid subfamily Cnemophilinae and with the Ptilono-rhynchidae.

INTRODUCTION

In New Zealand exists (or existed, as the case may be) a singular passerine bird that up to the present has defied the attempts of taxonomists to find a comfortable place for it among the recognised families of oscines. The Maoris called it Piopio; ornithologists recognise it under the generic name *Turnagra;* and it has otherwise had the unfortunate sobriquet of " New Zealand thrush." There are two distinct forms of *Turnagra: capensis* of the South Island and adjacent islets and *tanagra* of the North Island. These have been regarded either as two distinct species or as races of a single species, *capensis.* In this paper the two forms are treated binomially; generalisations about " *Turnagra* " apply to both forms. Regrettably, both of these species are now apparently extinct (Mills & Williams 1979). Using study skins and the little anatomical material that was preserved, we undertook an investigation of *Turnagra* to determine its relationships among the large and diverse group of oscine passerines.

TAXONOMIC HISTORY

Although originally described by Sparrman (1787) as *Tanagra capensis,* no modern taxonomist has considered the species to belong to the New World family Thraupidae (tanagers); Linnaeus and his contemporaries used the generic name *Tanagra* for a world-wide miscellany of birds with similar bill shapes. The specific name *capensis* was based on the mistaken belief that the bird came from South Africa.

The genus *Turnagra* was proposed for *capensis* by Lesson in 1837. *Keropia* Gray, 1840, and *Otagon* Bonaparte, 1850, are junior synonyms encountered in the early literature. We shall attempt to

review here only the more important opinions concerning the placement
of *Turnagra,* as in many of the early classifications the genus was
associated with several different artificial groups of birds before family
limits became somewhat stabilised.

As early as 1869, Buller put the North Island form of *Turnagra*
under the family Turdidae (thrushes), although without stating his
reasons at the time.   Sundevall (1872), using rather dubious external
characters (but perhaps to better effect than many of his successors),
placed *Turnagra* in his family Ptilorhynchinae *(sic),* in which he
included the bowerbirds *Ailuroedus, Ptilonorhynchus, Chlamydera,* and
Sericulus, as well as the Australian genera *Struthidea,* currently placed
in the Grallinidae, and *Cinclosoma,* a genus perhaps more problematical
than *Turnagra* but not thought to be closely related to the Ptilono-
rhynchidae.   Finsch (1872) had placed *Turnagra* in the Corvidae under
the subfamily Glaucopinae (= the modern Callaeidae) but later (1874)
transferred it to the Ptilonorhynchidae in deference to Sundevall.
Although these actions had merit, as we shall see, this allocation of
Turnagra was not generally adopted, probably because the whole of
Sundevall's classification was soon discredited (see Newton, 1896:
intro. 88-90).

To Buller and Hans Gadow we must credit most of the con-
fusion concerning the relationships of *Turnagra.*   In 1887 (p. 30)
Buller wrote: " Mr. Sharpe has placed *Turnagra* among his Timeliidae;
but I have decided to make it the type of a new family, Turnagridae,
because the form seems to differ quite as much from typical *Timelia*
as it does from *Turdus."*   Buller went on to quote extensively from
the anatomical notes supplied to him by Hans Gadow, whose con-
clusions were as follows:

> After examination of the digestive apparatus, the pelvic
> nerve-plexus, the skeleton, and the pterylosis, I feel inclined to put
> **Turnagra** with the wide and ill-defined group of Timeliidae. **Turnagra**
> is certainly neither Corvine nor Fringilline, and it is in fact a member
> of the Southern (Indian Australian) mass of Thrush-like birds.   Its
> bill and certain modifications of its digestive apparatus seem to
> show that this bird is a **Thrush with graminivorous propensities**
> [emphasis Gadow's].   I would put it into Sharpe's subfamily
> Ptilonorhynchidae, to which **AEluroedus** belongs, but unfortunately
> **Ptilonorhynchus** itself is very different from Timeliidae in its
> pterylosis.

Upon reading this passage, a modern ornithologist could hardly
be faulted for having not the least idea of the true affinities of
Turnagra, as no fewer than three currently recognised " families "
of passerines are alluded to — Turdidae, Timaliidae, and Ptilono-
rhynchidae.   Even today, the " family " Timaliidae is regarded as a
poorly defined group, and in Sharpe's time it was an even more
heterogeneous conglomeration, being described as a " refuge for the
destitute " containing a great many forms that " cannot . . . be con-
veniently stowed elsewhere " (Newton 1896: 25).   Despite the am-

biguity of Gadow's conclusion, it was doubtless his continued allusion to thrushes that kept the Turdidae under consideration for so long. This is but another of many examples of how uncritical acceptance of Gadow's preliminary examinations became fixed in the literature for generations (as with *Pedionomus,* for example — Olson & Steadman 1981).

Buller's writing (1887) further associated *Turnagra* with the word " thrush " and at the same time influenced subsequent classifiers to regard *Turnagra* as forming a monotypic family, an action that did little to elucidate the relationships of the genus. Oliver (1930) originally adopted the use of Turnagridae and cited the above quotation from Gadow *(in* Buller 1887), but later he showed that the palate of *Turnagra* was not similar to that of *Turdus* and recommended that *Turnagra* " be placed in the neighbourhood of *Gymnorhina* [Cracticidae] " (Oliver 1945: 148).

Mayr & Amadon (1951: 20) stated that *Turnagra* probably belonged in the Pachycephalinae rather than in the Turdinae, citing Oliver's observation that the skull is very different from that of *Turdus,* but without giving reasons for allying the genus with *Pachycephala* and its presumed relatives. Oliver (1955: 524) countered Mayr & Amadon, stating that the palate of *Turnagra*

. . . differs essentially from that of the true thrushes, and also from that of the thickheads **(Pachycephala)** with which **Turnagra** has recently been allied. The maxillo-palatines meet in front of the vomer as they do in the Australian Magpie **(Gymnorhina)** and the Manucode **(Manucodia).** Accordingly I have removed the family Turnagridae from the neighbourhood of the thrushes. . . . Finsch placed **Turnagra** with the bower birds, a much better position than with the thrushes.

Finsch's arrangement, as we have seen, is properly attributed to Sundevall.

On the basis of Oliver's work, the OSNZ Checklist Committee (1953: 68) retained *Turnagra* " in a separate family, near the Cracticidae (Bell Magpies) and Ptilonorhynchidae (Bower Birds) " and this treatment was followed in the subsequent edition (1970). Mayr (1967: 52) placed *Turnagra* as a genus *incertae sedis* after the Pachycephalinae, noting that it was " of uncertain affinity but more similar to the whistlers than to the thrushes where the genus is often placed." Ames (1975: 127) briefly reviewed the taxonomic history of *Turnagra,* concluding that it " is now usually regarded as [a] non-thrush of uncertain affinities." He observed that the generalised oscine syrinx of *Turnagra* is unlike the diagnostically specialised syrinx of the Turnidae.

Our study was initiated in 1975, when Olson, who was familiar with specimens of *Turnagra capensis,* first chanced to examine skins of the Tooth-billed Bowerbird *(Scenopoeetes dentirostris).* He was immediately struck by the great resemblance in colour and pattern of these two species. This sparked our collaborative effort and we pre-

FIGURE 1 — Ventral view of study skins of **Turnagra capensis** (left) and the Tooth-billed Bowerbird, **Scenopoeetes dentirostris,** to show the great similarity in plumage pattern

sented our conclusions at a meeting later in the same year (American Ornithologists' Union, Winnipeg). Since then, both Fleming (1982) and Sibson (1982) have mentioned a possible connection between *Turnagra* and the bowerbirds, particularly *Scenopoeetes,* citing behavioural as well as external morphological evidence. Fleming's suggestion, and probably Sibson's as well, stems from unpublished observations of D. H. Brathwaite and K. A. Hindwood dating back to 1968.

That our discovery of similarities between *Turnagra* and *Scenopoeetes* was completely independent is testimony to the strength of the resemblances between these two genera.

The present paper attempts to support the hypothesis of relationship between *Turnagra* and the bowerbird group on the basis of different aspects of morphology. Parkes, who had already become interested in variation within *Turnagra* (Parkes, MS), undertook the comparisons of external morphology. Clench, who had made detailed studies of the pterylosis of bowerbirds in another connection, provided a comparison of the pterylosis of *Turnagra* with that of several of the suggested relatives of the genus. Borecky's PhD dissertation at the University of Pittsburgh (1977) deals with the appendicular myology and relationships of the so-called " corvid assemblage." In the course of his investigations, he was able to dissect a specimen of *Turnagra* to determine whether appendicular myology could throw any light on the relationships of the genus. Olson is responsible for the osteological comparisons, the taxonomic history, and the final organisation and preparation of the manuscript.

EXTERNAL CHARACTERS

We have alluded above to the striking general resemblance in plumage pattern between *Turnagra capensis* and *Scenopoeetes dentirostris* (Fig. 1). General proportions of the two are also quite similar. We also noted the following additional similarities in epidermal structures: tarsal scutellation; wing formula; relative development of chin, rictal, and nasal bristles; and a series of slight grooves anterior to the nostrils in most specimens. The yellow eye has also been cited as resembling bowerbirds of the genera *Sericulus* and *Prionodura* (Fleming 1982).

The heavy toothed bill of *Scenopoeetes* differs markedly from the relatively unspecialised bill of *Turnagra,* but likewise from that of all other bowerbirds. The bill of *Turnagra,* on the other hand, is very similar to that of bowerbirds such as *Amblyornis* (Fig. 2). The tail of *Turnagra* is proportionately longer than that of *Scenopoeetes* but no more so than in *Chlamydera* or *Prionodura.* In both *Turnagra* and *Scenopoeetes* the two outermost primaries (P-10, P-9) are straight edged; *Turnagra* then has the next three primaries, and *Scenopoeetes* the next four primaries, with sinuated outer webs.

Only two specimens in the AMNH series of *Scenopoeetes* have remnants of an " immature " plumage. These plumage remnants show characters resembling *Turnagra capensis* as follows: dark barring or edging of under tail-coverts fainter or lacking in immatures; the upper wing-coverts that are broadly rufous-edged in *T. capensis* are narrowly edged with pale rufous (specimens worn and faded) in *Scenopoeetes* (wholly lacking in adults); in what appears to be the younger specimen of *Scenopoeetes* (AMNH 697435) the ear coverts are somewhat more rufescent, less dark olive-brown than in adults, recalling the more rufous face of most young *Turnagra capensis.*

FIGURE 2 — Lateral view of study skins of the Tooth-billed Bowerbird, **Scenopoeetes dentirostris** (top), **Turnagra capensis** (middle), and a more typical bowerbird, **Amblyornis macgregoriae** (bottom). Whereas the heavy bill of **Scenopoeetes** is distinctive, the bill of **Turnagra** is similar to that found in other bowerbirds.

One of the most interesting similarities between *Turnagra* and bowerbirds is the fairly frequent occurrence of asymmetrical central rectrices. In *Turnagra capensis* AMNH 591959, for example, both central rectrices are fresh and unsheathed; R-1 is about 5.5 mm longer than L-1. It should be stressed that *all* of these rectrices are of " adult " shape; in *Turnagra,* " immature " rectrices are longer, and narrower, than " adult" rectrices (Parkes, MS). In one of the two apparent first-year specimens of *Scenopoeetes* (AMNH 679435), R-1 is about 13 mm shorter than L-1, with no evidence (basal sheathing) of continuing growth. In a presumed adult (AMNH 679422), R-1 is about 3.5 mm shorter than L-1. This phenomenon occurs in other bowerbirds as well. In three adult males of *Amblyornis macgregoriae mayri* (AMNH 679533, 679529, 342276), R-1 is about 8 mm, 3.5 mm, and 5.5 mm shorter than L-1, respectively, with no sheathing at the base of the shorter rectrix. An adult male of *Archboldia papuensis sanfordi* (AMNH 705705) shows R-1 about 8 mm shorter than L-1, again with no sheathing at the base.

The significance of the occasional appearance of asymmetrical central rectrices in *Turnagra* and bowerbirds is not clear, but that it may indicate relationship is suggested by examination of the 101 specimens of Pachycephalinae in the Carnegie Museum, none of which shows more than 1 mm difference in length between R-1 and L-1.

COMPARATIVE PTERYLOSIS OF *TURNAGRA*

Unfortunately, the study of the body pterylosis (feather tracts) of *Turnagra* is hampered by the lack of adequate material. The only two known spirit specimens are both badly damaged by shot and one is in heavy moult. We probably should not complain, however, for like most rare and interesting birds, if they had not been poor specimens when collected they undoubtedly would have been made into study skins rather than anatomical specimens. It is also unfortunate that a spirit specimen of *Scenopoeetes* does not exist, although we were able to study the gross aspects of its pterylosis in an unstuffed study skin at the AMNH.

The general body pterylosis of *Turnagra* is clearly more similar to the kinds of patterns and density of feathering found in members of the bird-of-paradise/bowerbird assemblage than to those of the Muscicapidae *(sensu lato)* or other oscines. The dorsal tract exhibits most of the taxonomically interesting variation and in *Turnagra* is very heavily feathered, with an exceptionally dense saddle composed of approximately 15 rows containing a total of about 300-327 feathers (2 specimens). No saddle apterium is apparent, but the condition of both specimens does not preclude the possibility of a very small apterium at the posterior end of the element. The ventral tract is also heavily feathered and of typically oscine configuration.

In contrast, the saddles of thrushes are much more lightly feathered, averaging about half as many feathers (counts of 141-184

in nine or ten rows: 8 specimens of 5 species of 3 genera, including *Turdus*). A specimen of *Pachycephala flavifrons* (Pachycephalinae) was found to have a typically oscine saddle of 117 feathers in nine rows. A poor specimen of *Lamprolia victoriae* also had a typically oscine saddle, with nine or ten rows and no apterium; overall it was very like *Pachycephala* and *Muscicapa*. Although the saddles of corvids are of a different pattern, they are relatively lightly feathered, with counts ranging from 50 in six rows for *Platylophus*, to 198 in 12 rows for a Common Raven *(Corvus corax)*; 15 other genera are intermediate in number (114-178). Nor do the Cracticidae or Grallinidae have notably heavy saddles. One specimen of *Cracticus* has 10 saddle rows, and *Grallina* and *Struthidea* have 9, versus 15 in *Turnagra*. Two specimens of Callaeidae *(Heterolocha* and *Callaeas)* both have saddles containing 298 feathers in 14 rows, which is comparable to *Turnagra's* 300-327 in 15. Pattern differences in the saddle, and especially in the ventral tract, however, argue against a close relationship between *Turnagra* and the Callaeidae.

Within the bird-of-paradise/bowerbird complex, several patterns and degrees of feathering occur. Of the bowerbirds available as fresh or spirit specimens *(Ailuroedus, Amblyornis, Sericulus, Ptilonorhynchus.* and *Chlamydera)*, all have heavy saddles, with 180-281 feathers, ranging from 11 to 15 rows long; the single study skin of *Scenopoeetes* also has a heavily feathered saddle. The pattern of bowerbird saddles differs from that of most oscines, however, in that a long and conspicuous apterium is present at the base; *Scenopoeetes* has such an apterium. Saddle apteria of various sizes also occur in almost all corvids, and in *Grallina* (but not in *Struthidea* or *Corcorax)*, in some cracids, and a few other oscines (Clench, MS).

The birds-of-paradise show a strong dichotomy in both dorsal and ventral tracts. The " typical " genera (subfamily Paradisaeinae, of which we have examined 14 of 17 genera as fresh or spirit specimens) have strikingly sparse feathering. Saddles range from 7 to 10 rows in length, with 83-180 feathers; *Astrapia* differs somewhat with 200 or 201 feathers in 11 rows. Typical birds-of-paradise also have a distinctive and characteristic pattern at the base of the saddle — a wide spacing of the central feathers, giving the appearance of a small apterium. *Astrapia* is similar, but it also lacks the central feather of the posterior-most row and hence has a true, if very small, apterium.

Of the other subfamily of paradisaeids (Cnemophilinae), which Bock (1963) considered to represent the ancestral stock of both the Paradisaeinae and the Ptilonorhynchidae, we have examined all three genera — *Loria* in detail and *Cnemophilus* and *Loboparadisaea* in poor specimens. *Loria* exhibits a strong contrast to the typical birds-of-paradise in that it has a long and heavy saddle — 225-254 feathers in 13 rows (two specimens). *Cnemophilus* and *Loboparadisaea* are similarly heavily feathered. None has the posterior saddle " weakness " characteristic of the Paradisaeinae. On the contrary, the cnemophilines show a definite pterylographic similarity to *Turnagra*.

In summary, with the comparative material at present available, the pterylosis of *Turnagra* strongly suggests that this genus belongs in the bird-of-paradise/bowerbird assemblage rather than in the Muscicapidae *(sensu lato)*. Within this assemblage it is most closely similar to the members of the Cnemophilinae.

MYOLOGY

In his study of the so-called "corvid assemblage," Borecky (1977) compared the appendicular myology of *Turnagra capensis* with that of representatives of five genera of Ptilonorhynchidae *(Ailuroedus, Amblyornis, Sericulus, Ptilonorhynchus,* and *Chlamydera)* and nine genera of Paradisaeidae *(Loria, Manucodia, Semioptera, Epimachus, Astrapia, Parotia, Cicinnurus, Diphyllodes,* and *Paradisaea)*. Because Mayr (1967) placed *Turnagra* near the Pachycephalinae, the hindlimb myology of *Pachycephala* and *Hylocitrea* was also examined for the present study.

In *Pachycephala* and *Hylocitrea,* M. obturatorius lateralis pars dorsalis is relatively small and has a fleshy insertion on the tendon of M. obturatorius medialis and the head of the femur. This is the
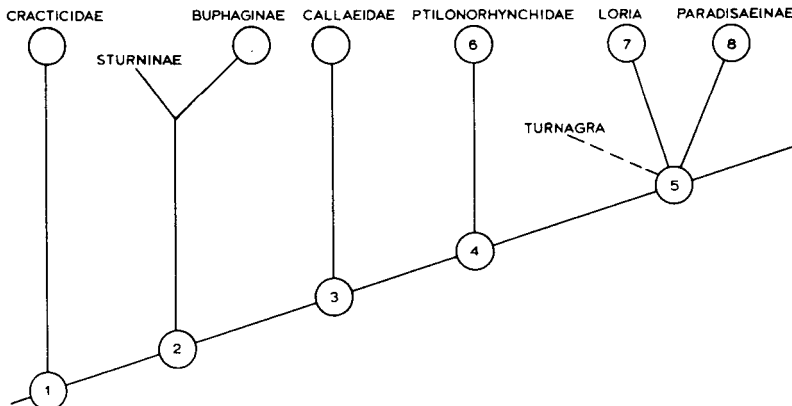

FIGURE 3 — Phylogenetic affinities as proposed by Borecky (1977) on the basis of myology (modified so as to omit characters not pertinent to the present discussion). (1) M. obturatorius lateralis pars dorsalis relatively large and inserting tendinously on the femur; (2) M. flexor perforatus digiti II is not perforated by the tendon of M. flexor digitorum longus; (3) M. iliofemoralis externus present (Type 1); (4) M. flexor hallucis brevis large; (5) Type 2 M. iliofemoralis externus present and reversal of M. flexor perforatus digiti II to the bifurcate and perforate condition; (6) M. deltoideus minor arising from the scapula and coracoid; (7) M. deltoideus minor arising from the scapula and coracoid; (8) Type 3 M. iliofemoralis externus present and femoral head of origin of M. flexor digitorum longus present.

primitive condition.   In *Turnagra,* the Paradisaeidae, Ptilonorhynchidae and certain other families, M. obturatorius lateralis pars dorsalis is relatively large and inserts by means of a tendon on the head of the femur just cranial to the insertion of M. obturatorius medialis (character 1 in Fig. 3). *Pachycephala* and *Hylocitrea* lack M. iliofemoralis externus, which is present in *Turnagra,* the Callaeidae, Ptilonorhynchidae, and Paradisaeidae (character 3 in Fig. 3).   The presence of this muscle in passerine birds represents a derived character state (Borecky 1977). *Turnagra* shares no derived myological features with the two members of the Pachycephalinae examined and therefore it should not be in-cluded in that group.

Because *Turnagra* possesses the Type 2 configuration of M. iliofemoralis externus, a trait otherwise observed only in *Loria,* Borecky (1977) provisionally placed *Turnagra* near the Paradisaeidae (Fig. 3). This, however, is in conflict with the fact that *Turnagra* lacks an enlarged M. flexor hallucis brevis, a derived condition shared by the Ptilonorhynchidae and Paradisaeidae (character 4 in Fig. 3).   In *Turnagra, Ailuroedus,* and *Chlamydera* (Ptilonorhynchidae), the tendon
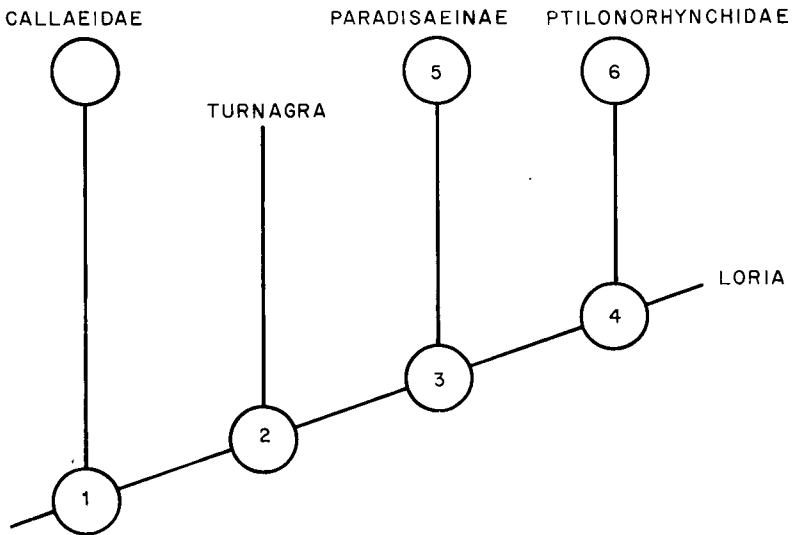
FIGURE 4 — Alternative phylogeny using the same myological characters. as Borecky (1977).   (1) Type 1 M. iliofemoralis externus present; (2) Type 2 M. iliofemoralis externus present; (3) M. flexor hallucis brevis large and reversal of M. flexor perforatus digiti II to the bifurcate and perforate condition; (4) M. deltoideus minor arising from the scapula and coracoid; (5) Type 3 M. iliofemoralis externus present and femoral head of origin of M. flexor digitorum longus present; (6) reappearance of Type 1 M. iliofemoralis externus.

of insertion of M. flexor perforatus digiti II is not perforated by the tendon of M. flexor digitorum longus. This is a derived condition (character 2 in Fig. 3) that is assumed to have reversed to the primitive state in the Paradisaeidae (part of character suite 5 in Fig. 3), but because such a reversal must also be postulated for the remainder of the Ptilonorhynchidae as well as two of the three species of Grallinidae (Table 4 in Borecky 1977), the significance of this character is doubtful. M. flexor perforans et perforatus digiti II in *Turnagra* and *Ailuroedus* does not ensheath the tendon of M. flexor digitorum longus, which is a derived condition suggesting that *Turnagra* may be allied to the bowerbirds.

An alternative phylogeny can be suggested from the same characters (Fig. 4). In this, *Turnagra* would branch off before the Paradisaeidae and Ptilonorhynchidae to reflect the fact that it does not have an enlarged M. flexor hallucis brevis (part of character suite 3 in Fig. 4). With the arrangement proposed here, the derived condition of M. deltoideus minor would define the Cnemophilinae and Ptilonorhynchidae as a monophyletic group (character 4 in Fig. 4), instead of evolving independently in these lineages (characters 6 and 7, which are the same, in Fig. 3). This has the disadvantage of requiring the Type 1 condition of M. iliofemoralis externus to reappear in the Ptilonorhynchidae. This is conceivable, however, as such a reappearance presumably also took place in the Paradisaeinae, where *Epimachus* has the Type 1 condition and the other species have Type 3.

Each of the phylogenies proposed on the basis of myology requires several reversals or reappearances of characters. Although that in Fig. 4 may require fewer, neither is entirely satisfactory, suggesting that these few variable myological characters may be inadequate for resolving branching sequences within the bird-of-paradise/bowerbird assemblage, particularly in the absence of myological information on members of the Cnemophilinae other than *Loria* and of ptilonorhynchids such as *Scenopoeetes.*

Although the appendicular myology of *Turnagra* strongly suggests that it is a member of the bird-of-paradise/bowerbird assemblage, it does not clearly indicate that *Turnagra* belongs with either the Ptilonorhynchidae or the Paradisaeidae, as presently defined. If the Type 2 M. iliofemoralis externus is a derived character state within this assemblage, this would suggest that *Turnagra* is closely allied to the Cnemophilinae, as exemplified by *Loria*. On the other hand, the patterns of insertion of M. flexor perforatus digiti II and M. flexor perforans et perforatus digiti II might suggest that it is more closely allied to some members of the Ptilonorhynchidae.

OSTEOLOGY

Our osteological studies included three unsexed skeletons of *Turnagra,* none of which has data or is certainly identified as being one or the other of the two forms of the genus. These specimens are

TABLE 1 — Measurements of the three known skeletons of **Turnagra**. Because of its larger size and characters of the bill, the NMNZ specimen is presumed to be **T. tanagra** and the other two are presumed to be **T. capensis.** * = damaged.

	NMNZ 15080	MCZ 1349	ANSP 38708
Total length of skull	50.9	47.2	45.5
Length of bill from naso-frontal hinge	25.1	22.4	21.8
Width of cranium at postorbital processes	23.3	20.6	----
Width of bill at posterior margin of nostrils	12.6	11.0	10.2
Length of mandible	38.0	34.2	33.9
Length of mandibular symphysis	11*	10.0	9.2
Width of mandibular symphysis at posterior margin	9.2	7.5	7.2
Length of sternal carina	29.6	26.9	27.0
Width of sternum at articulation of last rib	16.2	14.9	14.6
Length of ilium	30.8	30.0	28.8
Width of pelvis across antitrochanters	22.1	21.8	----
Length of coracoid	27.7	24.7	24.0
Length of humerus	33.0	----	31.0
Length of ulna	35.8	----	33.4
Length of carpometacarpus	19.7	----	17.5
Length of femur	33.2*	32.9	----
Length of tibiotarsus	55.3	51.8	----
Length of tarsometatarsus	40.1	36.8	----

as follows: National Museum of New Zealand 15080, Museum of Comparative Zoology 1349, and Academy of Natural Sciences of Philadelphia 38708 (lacking both hindlimbs).

The NMNZ specimen differs considerably from the other two in size (Table 1) and in the following skull characters: (1) all portions of the palatines wider; (2) posterior portion of palatines rounded, without transpalatine processes (possibly broken, but if so this was not evident under magnification and furthermore the right and left palatines are identical to each other); (3) pterygoids noticeably wider; (4) zygomatic process thicker; (5) lacrimo-ectethmoid complex much more inflated; (6) bill deeper, appearing proportionately shorter; (7) internarial bar more robust. The larger size and more robust bill of this specimen suggests that it may be *Turnagra tanagra,* the North Island form, whereas the other two may be *Turnagra capensis.* The differences between the putative specimen of *tanagra* and the other two are considerable and, if constant, would certainly suggest that the two forms of *Turnagra* are specifically distinct.

The overall morphology of the skull of *Turnagra* is quite similar to that of bowerbirds such as *Ailuroedus* (Fig. 5). This applies to bill shape, proportions, and architecture of the palate. In the two smaller specimens that are probably *T. capensis,* there are well-developed transpalatine processes exactly resembling those of *Ailuroedus.* Such transpalatine processes were considered by Bock (1963) to be characteristic of bowerbirds, at least within the bird-of-paradise/bower-bird assemblage. In the one skull of *Scenopoeetes* that was available for this study, however, the transpalatine processes are absent and the posterior margins of the palatines are rounded, with a somewhat serrated edge (Fig. 6). The palatines in the skeleton of *Turnagra* cf. *tanagra* (Fig. 6) are like those of *Scenopoeetes* and quite different from the palatines in the other two specimens of *Turnagra* or of other bowerbirds. The significance of these differences is difficult to assess.

On the basis of osteology, plumage, and behaviour as described by Gilliard (1969), we see little justification for the recent trend towards submerging *Scenopoeetes* in *Ailuroedus,* as has been done in several recent Australian publications. *Scenopoeetes* appears to be quite distinct, and it is not particularly evident that *Ailuroedus* is necessarily closely related to it.

Turnagra differs from all bowerbirds in lacking large, free lacrimals and in having the zygomatic process better developed. In both these respects, however, *Turnagra* resembles the paradisaeid sub-family Cnemophilinae (*Macgregoria* only for the zygomatic — see Bock 1963). *Turnagra* appears to differ from the other taxa examined in having the maxillopalatines poorly ossified, being rather amorphous structures that are not easily separable from the surrounding cartilage.

The presence of a well-developed lacrimal bone in the Ptilono-rhynchidae would seemingly be the primitive condition, whereas its
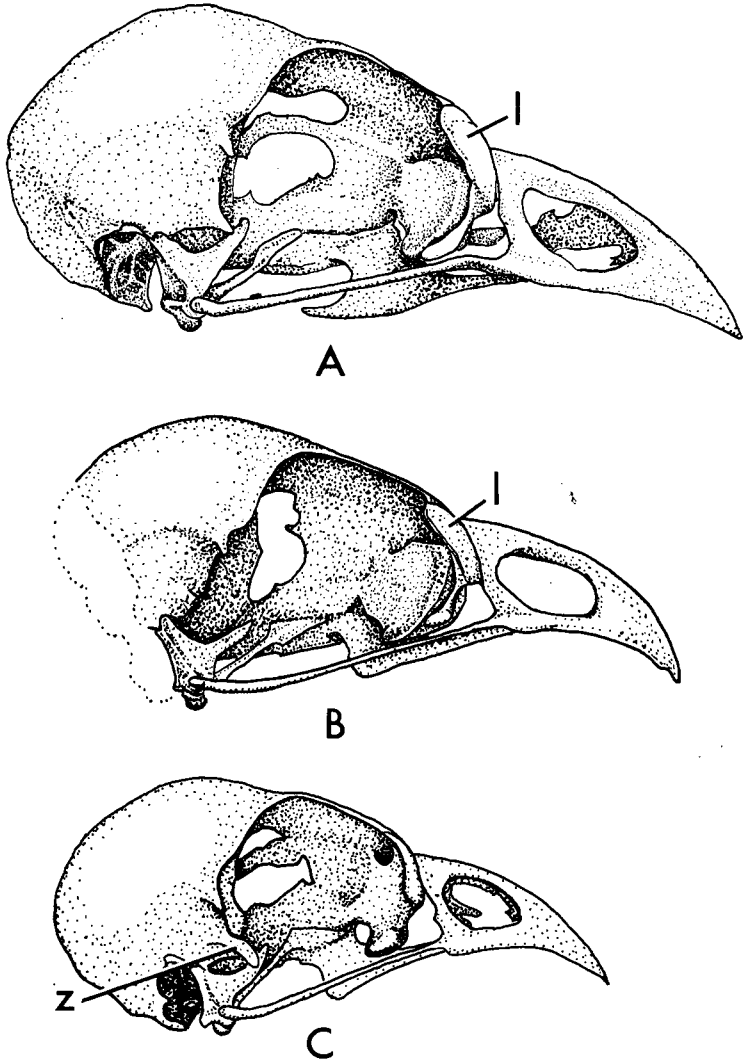
FIGURE 5 — Lateral view of the skull of (A) Green Catbird, **Ailuroedus crassirostris** (Ptilonorhynchidae); (B) Tooth-billed Bowerbird, **Scenopoeetes dentirostris** (Ptilonorhynchidae); (C) **Turnagra** sp. (the NMNZ specimen presumed to be **T. tanagra**). Although the skull of **Turnagra** is generally similar to that of bowerbirds, note the absence of the lacrimal (l) and the well-developed zygomatic process (z) of **Turnagra**, both of which characters are found in the Cnemophilinae.

loss would be derived. Bock's (1963) proposed phylogeny and that in Fig. 4 would require the evolutionary reappearance of this bone, which considering how many different myological traits must have reappeared, no matter how the various bowerbirds and birds-of-paradise are arranged, cannot flatly be ruled out. On the other hand, it does appear that in other passerines (e.g. Rhinocryptidae) the lacrimal may be incorporated into the ectethmoid and eventually obliterated (Feduccia & Olson 1982). Thus, it is not possible at this point to say whether the absence of a lacrimal in *Turnagra* is primitive or derived. In overall similarity, *Turnagra* would have to be said to resemble the Cnemophilinae more than the Ptilonorhynchidae in this respect.

The Pachycephalinae was included in the comparisons because of Mayr's (1967) placement of *Turnagra* near that group. The skull of *Turnagra* agrees with that of the bowerbirds and differs from *Pachycephala* as follows: (1) rostrum much heavier and more decurved; (2) premaxillary symphysis longer; (3) nasal bar stouter; (4) partially ossified nasal septum present; (5) ventral surface of premaxillary symphysis more excavated, with a distinct median ridge; (6) nostril relatively shorter and deeper; (7) orbital process of quadrate much longer. The skull of *Turnagra* therefore does not suggest a close affinity with *Pachycephala.* On the other hand, it shows considerable similarity to the Ptilonorhynchidae and the Cnemophilinae, and nothing in its structure would preclude *Turnagra* from being associated with the bird-of-paradise/bowerbird assemblage.

CONCLUSIONS

Derived characters of myology and pterylosis indicate that *Turnagra* belongs in the bird-of-paradise/bowerbird assemblage. The osteology, external morphology, and plumage characters of *Turnagra* are compatible with this placement, whereas we found no anatomical or plumage characters that would support a relationship between *Turnagra* and the Pachycephalinae.

The greatest remaining difficulty is deciding where *Turnagra* best fits within the bird-of-paradise/bowerbird assemblage, as there is considerable conflict among the various characters. In the pterylosis and some myological and osteological characters, the greatest similarity is to the Cnemophilinae. In plumage pattern, overall external appearance, and in other osteological and myological characters there is greater similarity between *Turnagra* and the Ptilonorhynchidae. *Turnagra* has none of the derived characters that define the Paradisaeinae and it may be safely assumed that the genus does not belong in that subfamily.

The small M. flexor hallucis brevis and rather generalised overall structure suggest that *Turnagra* may be the most primitive member of the bird-of-paradise/bowerbird assemblage and thus closest to the common ancestor of that group. This might help to explain the conflicting nature of many of its characters, *Turnagra* possibly
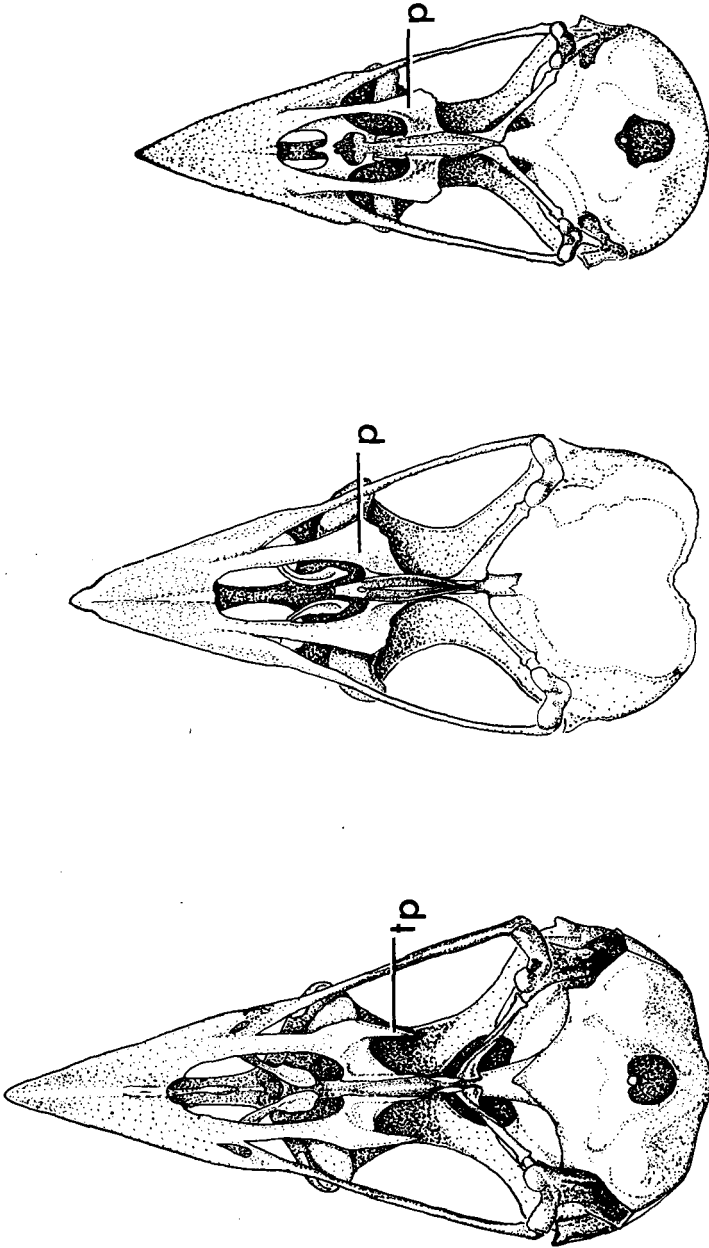
FIGURE 6 — Ventral view of skulls of (A) Green Catbird, *Ailuroedusc crassirostris* (Ptilonorhynchidae); (B) Tooth-billed Bowerbird, *Scenopoeetes dentirostris* (Ptilonorhynchidae); (C) *Turnagra* sp. (the NMNZ specimen presumed to be *T. tanagra*). Although the shape of the palatines (p) in *T. tanagra* is similar to that in *Scenopoeetes*, in the two skeletal specimens examined that are presumed to be *T. capensis* the transpalatine processes (tp) were well developed as in typical bowerbirds.

having branched off before the other groups evolved many of their distinctive features.

What, then, do we do with *Turnagra* taxonomically? We shall begin with the premise that monotypic families of passerines are highly undesirable. Maintaining a separate family Turnagridae cannot be justified on anatomical grounds because there are no derived characters by which such a family could be defined that are not found in some other member of the bird-of-paradise/bowerbird assemblage. Furthermore, this would do nothing to clarify the relationships of the bird. Until the branching pattern within the bird-of-paradise/ bowerbird assemblage can be worked out in better detail, it seems best to place all members of this assemblage in a single family, Paradisaeidae, with the Ptilonorhynchidae being reduced to a subfamily. Within this expanded family, *Turnagra* should be placed first, either without assigning it to a particular subfamily or maintaining it for the present as a separate subfamily, Turnagrinae. In addition, we applaud the current use by New Zealand ornithologists of the vernacular name Piopio and strongly recommend that the word " thrush " no longer be used for *Turnagra*.

As a member of the Paradisaeidae, in the broad sense, *Turnagra* demonstrates once again the intimate connection between the avifauna of New Zealand and that of Australia and New Guinea. It is of interest that there has been essentially no radiation of these birds in New Zealand, there being only two forms of *Turnagra,* which from their osteology appear to be distinct species.

ACKNOWLEDGEMENTS

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SHORT NOTES

EFFECT OF RAIN ON FANTAIL NEST-BUILDING

In my account of the breeding of the North Island Fantail *(Rhipidura fuliginosa placabilis)* in *Notornis* 12 (3), I suggested on p. 137 that " our fantail could possibly retain an ancestral response to factors other than increasing hours of daylight in the control of its breeding season," and I produced evidence to show that mild but heavy rain at the end of a dry winter induced nesting in the first few days of August 1959 in the two pairs of fantails around my home. Recent observations seem to support this view.

In May 1979, after heavy warm rain at the end of a dry spell, I watched a pair putting the finishing touches to a nest, although no eggs were laid in it. On 6 April 1983, just 2 days after a fall of 2½ inches, which broke 5 months of drought in the Gisborne-East Coast district, I saw fantails collecting nest-lining material from a *Dicksonia*

squarrosa. Over many years this tree fern, hard by our back door, has been the source of lining material for fantails from two territories, being just outside the limits of both territories.

In many Australian species, the urge to breed depends on adequate rainfall, and our fantail may have retained the instinct to nest, even though not necessarily to breed, after rain. According to Fleming *(Notornis* 9: 270), our fantail has descended from the Grey Fantail of Australia over some 20 000 years, developing only slight differences in plumage. Several authorities such as Serventy & Whittell in *Birds of Western Australia* and Pizzey in *A field guide to the birds of Australia* say that there is a post-breeding dispersal, or migration, to dry areas by the Grey Fantail; thus, the dependence on rainfall as a stimulus may have developed.

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APRIL BIRD-COUNTS AT OHAU GORGE NEAR LEVIN

In April 1982 I made 82 5-minute stationary bird-counts in the Ohau Gorge near Levin to obtain indices of abundance of the forest birds there. I counted on the track to the Ohau Shelter from 878 975 (NZMS1 N152) to 894 957. This route of about 2.8 km passes along the side of the gorge, or crosses flat terraces, on the south bank of the Ohau River at an altitude of about 200 m, well above the river. The mixed podocarp-hardwood forest is continuous with that of the Tararua State Forest Park. It has been modified by logging and by mammalian browsers. Many remaining emergents are dead or damaged.

I used Dawson and Bull's method of counting (1975, *Notornis* 22: 101-109). The counting-stations (not fixed) were at least 250 paces (200 m) apart, and the first was at least that distance from the forest edge. I walked a little further between stations to escape the sound of the river below if it was loud. I could make up to 12 or 13 counts in each direction. Counts were completed in fine weather (not wet or windy) between 1013h and 1529h (NZ Standard Time). The distribution of counts was 3rd of April (3 counts), 6th (23), 11th (10), 17th (25) and 24th (21).

The species encountered and total numbers seen plus heard during the counts were Grey Warbler *(Gerygone igata)* 57, Fantail *(Rhipidura fuliginosa)* 56, Tit *(Petroica macrocephala)* 44, Blackbird *(Turdus merula)* 22, Silvereye *(Zosterops lateralis)* 147, Bellbird *(Anthornis melanura)* 58, and unidentified 18. Table 1 gives the average numbers per count. Except for 7 Magpies *(Gymnorhina tibicen)*, I noted no other species during the counts, although I saw New Zealand Pigeons *(Hemiphaga novaeseelandiae)* at other times, and Riflemen *(Acanthisitta chloris)* occurred on nearby ridges.

Table 1 also shows average numbers per 5-minute count in kanuka forest at Kowhai Bush (near Kaikoura) in April 1977 (Gill 1980, *NZ J. Zool.* 7: 235-246), and in beech-podocarp forest at Fletcher Creek (near Reefton) in April 1974 (Dawson *et al.* 1978, *Notornis* 25: 257-278). There were no Tits, and Blackbirds were not counted, at Kowhai Bush. The differences between Ohau Gorge and Fletcher Creek for Tit and Blackbird were highly significant (chi-squared test; P <0.001). In 1 x 3 chi-squared tests the differences between areas were not significant for Grey Warbler (P >0.1) but highly significant for Fantail, Silvereye and Bellbird (P <0.001). In chi-squared tests between pairs of areas for these three species all differences were highly significant (P <0.001) except between Kowhai Bush and Ohau Gorge for Fantail and Silvereye (P >0.05). Therefore, all species except Grey Warbler were denser or more detectable at Fletcher Creek than elsewhere. No differences between Ohau Gorge and Kowhai Bush were significant, except for Bellbirds, which seem to have been denser in the kanuka forest.

There are several limitations to relying on counts for just one month as a general guide to the abundance of birds in an area. Five-minute counts are indices of abundance that reflect both abundance and detectability. Detectability may vary seasonally for each species. In comparing counts of a species for like months I have hoped that the contribution of detectability will be the same, but patterns of detectability for a species may vary between areas and years, making given months out of phase. Counts averaged over a whole year, with equal

TABLE 1 — Average 5-minute bird-counts in April at three lowland forests

Locality	Kowhai Bush	Ohau Gorge	Fletcher Creek
Altitude (m)	80	200	230
Year	1977	1982	1974
n (counts)	30	82	80
Grey Warbler	0.43	0.70	0.78
Fantail	0.40	0.68	1.38
Tit	0	0.54	1.51
Blackbird	—	0.27	0.66
Silvereye	1.33	1.79	2.89
Bellbird	1.87	0.71	3.34
Unidentified	0.40	0.22	—

effort throughout, may be preferable but are harder to achieve. At Fletcher Creek, Dawson *et al.* (1978) detected significant differences between April 1974 and April 1976 in the counts for nine of the eleven most abundant species. Besides difficulties with different years there are differences between observers, which Dawson *et al.* found to be statistically significant, though small.

If the figures in Table 1 are reliable, then the lowland forest of the Ohau Gorge compares very unfavourably, with that of north Westland, both in abundance of birds and in diversity — Tui *(Prosthemadera novaeseelandiae)*, Robin *(Petroica australis)*, New Zealand Pigeon, parakeet *(Cyanoramphus)* and Kaka *(Nestor meridionalis)* were counted at Fletcher Creek in April. Despite its lowland location, proximity to the sea (16 km) and continuity with a large tract of forest, the Ohau Gorge is not the prime habitat for forest birds that it probably once was. This may be partly because the forest is much modified and partly because it is a small and remnant lowland area in a block of forest that is mainly montane. That Ohau Gorge should seem to support lower densities of Bellbirds than kanuka forest is puzzling because many nectar-bearing plants present at Ohau Gorge (e.g. *Knightia, Alseuosmia*) are absent at Kowhai Bush, and within Kowhai Bush, Bellbirds seemed most numerous in an area with the densest and most diverse vegetation (Gill 1980).

I thank D. G. Dawson for commenting on a draft of this note, and Anne Wilson for typing the final manuscript.

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A CENTRAL OTAGO PECTORAL SANDPIPER

Seasonal flood-meadows with lush spring productivity are attractive places to waterfowl, wading birds and opportunistic species like the Pukeko *(Porphyrio p. melanotus)* and Spur-winged Plover *(Vanellus miles novaehollandiae)*.

'Taieri Lake,' 5 km from Kokonga, near Ranfurly, Central Otago, is such a habitat. It is the site where a suspected Japanese Snipe *(Gallinago hardwickii)* was seen some years ago and where the Glossy Ibis *(Plegadis falcinellus)* has been recorded on more than one occasion (see *Notornis* 16: 62).

In a good season, i.e. one with plenty of water, there are normally hundreds each of the common duck species (including Grey Teal *Anas gibberifrons gracilis)*, Spur-winged Plovers, Pied Stilt *(Himantopus h. leucocephalus)*, and South Island Pied Oystercatcher *(Haematopus ostralegus finschi)*, as well as smaller numbers of Pukeko, White-faced Heron *(Ardea novaehollandiae)*, Canada Goose *(Branta canadensis)*, Black Swan *(Cygnus atratus)*, with various other smaller species around the periphery and the ubiquitous Harrier *(Circus approximans gouldi)* scouting overhead. It is an area where prolonged and regular study

of many aspects such as seasonal changes, flocking, and moult would prove very rewarding.

Spring 1982 was a wet changeable season producing such favourable conditions, and when my wife and I visited this spot on Christmas Day the species listed were all present in substantial numbers. While I was walking around the soggy grassy perimeter of the ' free-standing ' water, a pipit-sized bird flew slowly past me into a fresh westerly breeze calling a fairly penetrating reedy *chirrrit*. Realising it was something unusual I followed its progress, and over the next hour and a half (during which it was flushed several times) we made the following observations.

Habits: Occasionally solitary, but tended to keep company with one or more Banded Dotterel *(Charadrius bicinctus)* on the shorter damp pasture beyond the zone of lush flood-meadow. Fed continuously, with a simple pecking motion, among the pasture grasses, not in water or muddy areas. Very alert, with slender neck periodically stretched up, giving it a tall appearance relative to the dotterels. It walked briskly but was not seen to run. It showed no aggression to the dotterels or to other species.

Size: Compared with the Banded Dotterels, about same height, tail somewhat longer, head much finer, neck and upper breast much slimmer; quite a different build.

Colouring: Rather drab above, overall appearance generally speckled greyish-brown; crown somewhat darker but plain. A pale greyish-white superciliary stripe with a grey-brown line through the eye. Speckles and streaks of paler grey-brown on upper breast ending in a fairly distinct demarcation separating this from the white of the underparts. No speckling visible on the flanks. Some variation in shades on the upper wing, but no pale wing-bar distinguishable in flight; underwing pale plain greyish-white. Rump dark brown medially with white side patches; upper tail dark brownish with blackish tips.

Bill: Slender, slightly longer than head, straight with a slight suggestion of decurvature throughout its length, mostly blackish but with yellowish flesh at the base.

Legs: Difficult to determine among the grass, but we eventually decided they were pale brownish or yellowish olive; did not extend beyond the tail in flight.

Voice: The only call heard, usually singly but on one occasion three times in succession, was the reedy *chirrrit*.

Because of the general colouring (lacking rufous tinges which characterise *C. acuminata)*, breast demarcation, stance and attraction to marshland, we concluded that this was a Pectoral Sandpiper *(Calidris melanotos)*.

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ALBINISTIC WHITE-FACED HERONS

Although the amount of white on the face of the White-faced Heron *(Ardea novaehollandiae)* can be quite variable, especially on young birds, four birds have been seen in Northland with much more white than usual.

1. The bird shown in Fig. 1 had least white of all. This photograph is one of several fine colour pictures taken by P. Morrin of Raupunga, Hawkes Bay, over 10 days in early July 1979 at Sandspit, Warkworth, using an 800 mm lens from a canoe. The bird was adult, as is shown by the long back plumes and the long buffy feathers on the breast. It was seen only at low tide and usually kept to itself, even though other White-faced Herons were present.

2. Marion E. Wallis of Maungaturoto saw two White-faced Herons with " head and breast snowy white " roosting in mangroves and in flight among c.20 normal White-faced Herons in the Herekino district on 4 April 1981. Bill, legs, wings, and rest of plumage were normal.

3. The bird shown in Fig. 2 was photographed by P. Morrin at Morumoru, north of Wairoa, on 10 June 1982. It was first reported by K. Hawkins, NZ Wildlife Service, in early June, and it could not be found again in July.

4. A bird reported to A. T. Edgar in mid-January 1981 by Mrs Susan Evans of Scudders Bay, Kerikeri Inlet, was on the Scudders Bay property of Dr J. F. Comely until at least mid-June, apart from a 2-week absence in late April. The pattern of white on this bird caused some dispute as to whether or not it was a White-necked Heron *(A. pacifica)*, which is only a rare vagrant to New Zealand. On 17 January, it was watched by a party that included ATE, BDH, and M. A. Kennedy. It seemed different from the other White-faced Herons nearby in several ways, which at least superficially suggested the field characters of White-necked Heron. The whole head and neck, including the long feathers of the lower neck, were white, except for several small pale-grey patches on the sides of the neck. Each wing had two white patches, one at the carpal bend and one (the larger) in mid-wing; the outlines of these patches were irregular, making the wing look patchy in flight. The bill was grey, black near the tip, facial skin grey, and iris, legs and feet were yellow. The rest of the plumage was like that of White-faced Herons.

This bird seemed larger, though not greatly so, than the other White-faced Herons it was near, in particular looking thicker and longer in neck and leg. When feeding on pasture, it held the head erect, often stretched at 45°, looking rather 'goose-like as it walked up a steep slope of pasture, taking earthworms after rapid but slight sideways movements of head and neck.

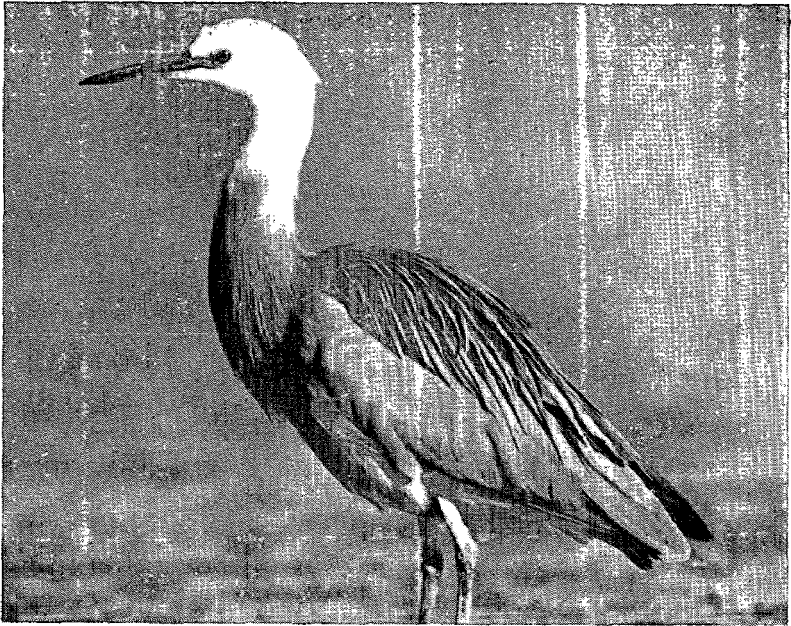On 19 January, BDH and MAK studied the bird closely by 25x

FIGURE 1 — White-faced Heron at Sandspit, Warkworth, July 1979.
Photo: P. Morrin

telescope as it sat and preened on a fence post near a normal White-faced Heron on another post. Apart from the white areas and the impression of slightly larger size, every detail of plumage was that of a White-faced Heron. Buff was lacking on the breast and the back plumes were not full length, and so the bird may not have been adult; it was in body moult because many white feathers were discarded during preening. Apart from the white areas, the grey patterns of upper wing, tail, and underparts were those of White-faced Herons. On several occasions, White-faced Herons were antagonistic to it.

Dr Comely noted that, although it fed in the same ways as the other herons, on the mudflats at low tide and the fields at higher tides, and roosted as they did at the tops of mangroves, it tended to keep to certain parts of both mudflats and fields and often roosted alone. It was usually accepted by the other herons but, when roused, often took wing first, possibly because its longer neck gave it better visibility. Its wing beats seemed to be slower and it tended to fly more and glide less than the other herons.

A distant but clear photograph of the bird taken by Dr Comely was shown to J. L. McKean of Darwin, who confirmed its identity as

FIGURE 2 — White-faced Heron near Wairoa, June 1982
Photo: P. Morrin

an albinistic White-faced.   The White-necked is very much larger and heavier billed, quite apart from many differences of plumage, especially in young birds.

In January 1983, the same bird was seen again by BDH and MAK.   It had become very much whiter, having wholly white head, neck, and mantle, and most of the wing surfaces were white.   The bird had been seen quite regularly by Dr Comely since 1981 and is presumably still there.

B. D. HEATHER, *10 Jocelyn Crescent, Silverstream*

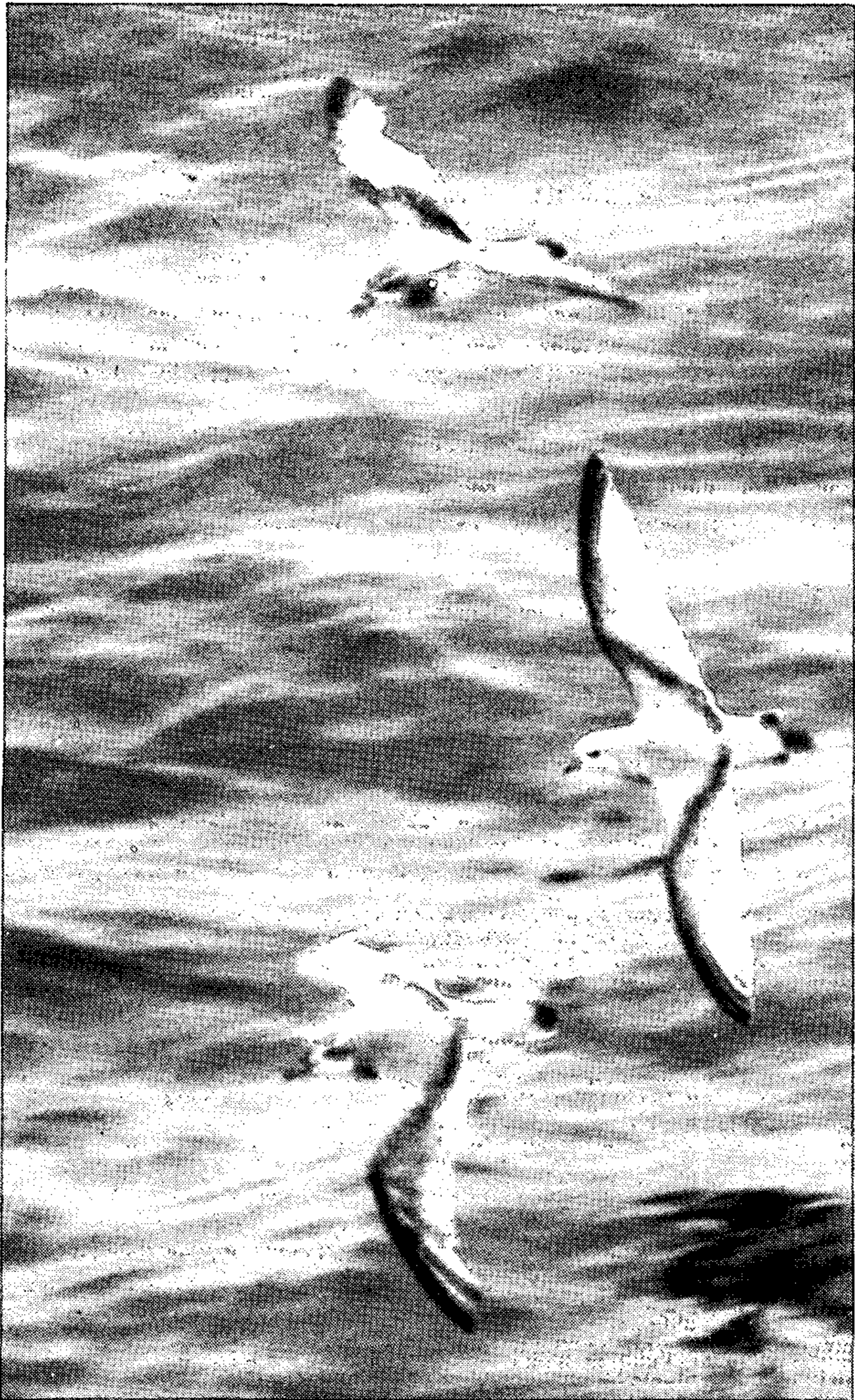# A PRION PICTURE PUZZLE FROM THE SOUTH ATLANTIC

FIGURE 1

FIGURE 2

During January and February 1982, while acting as an International Whaling Commission observer aboard the Russian research vessel *Vdumchiviy No 34,* Richard Rowlett took many photographs of seabirds. Four of his prion photographs are reproduced here from 35-mm colour slides.

Figure 1: Near the Antarctic Convergence north-east of Bouvetoya Island, 8 February 1982; three prions in flight. The upper and lower birds are Antarctic Prions *(Pachyptila desolata)* in worn plumage and wing moult. Note the large bill and the dark head and neck collar; also the central semicircle of dark feathers at the tail tip (cf. Fig. 3).

The middle bird is interesting. Note the short small bill and pale plumage, particularly the much paler head and neck region than on the *desolata.* The tail is moulting. The blurred central feathers are old rectrices; the adjacent dark spots are new rectrices yet to grow beyond the white tips of the undertail coverts visible in the photograph.

FIGURE 3

Figure 2: The same mystery bird. Note the position of the feet well forward of the central rectrices. Note also the exposed white undertail coverts and the pale fringing of the secondaries, the greater secondary coverts, and the inner primary feathers. The plumage is typical of immature birds.

Figure 3: An Antarctic Prion, near the Antarctic Convergence north-east of Bouvetoya Island, 8 February 1982. This is a classic example of a worn-plumaged adult bird in wing moult. The tail feathers are new. Such birds are abundant in the Scotia Sea region in February (Harper 1972).

FIGURE 4

Figure 4: A non-breeding Antarctic Prion, Weddell Sea, mid-January 1982. Note the fresh plumage, the dark head with smoky white superciliary, and the bill (cf. the slightly larger more heavily built Salvin's Prion *(P. salvini)* shown in Fig. 8 of Harper, 1980).

Discussion

So, what is the mystery bird?

A glance could easily have resulted in the Thin-billed Prion *(P. belcheri)* being entered in the logbook. It is common in the region, where it nests at the Falkland Islands (Strange 1980) and at the Crozets and Kerguelen (see Harper 1980).

However, the bill and facial pattern are clearly those of either the Fairy Prion *(P. turtur)* or the Fulmar Prion *(P. crassirostris)*.

Close examination of the photographs rules out males of *crassirostris* because the bill is too small. This leaves three possible candidates: a female of *crassirostris* (which is sexually dimorphic, females having smaller bills than males); the small subantarctic race of Fulmar Prion (at present known as *P. crassirostris eatoni* but the type specimen has been incorrectly identified: Harper, in prep.); and the Subantarctic Fairy Prion *(P. turtur subantarctica).* The very pale plumage of the photographed bird precludes the likelihood that it is a Fairy Prion *(P. turtur turtur).* In our opinion, the bird is a non-breeding Subantarctic Fairy Prion completing its first moult. It can be compared with the adult bird photographed off the Antipodes Islands illustrated in Harper (1980: Fig. 14).

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