

Seasonal movements and survival of royal spoonbill (*Platalea regia*) breeding in New Zealand

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Abstract Royal spoonbill (*Platalea regia*) nestlings ($n = 158$) were colour-banded between 1990 and 2005 at Green Island, Otago and Wairau lagoons, Marlborough. A total of 75% and 84% of Otago and Wairau birds, respectively, were resighted between 1991 and 2012. The pattern of independent resightings ($n = 737$) indicates that adult royal spoonbills in New Zealand undertake repeated seasonal inter-island migration, moving north to wintering sites (mainly Parengarenga, Rangaunu and Whangarei, up to 1200 km away), then relocating to the south again in summer to breeding sites. Most juveniles move as far north as adults, although a third of juveniles from Wairau were seen in winter in the Nelson region, a distance of < 100 km away. Juveniles and immatures (< 2 year old) remain in northern locations in summer, and return as adults (2 years and older) to their natal area. In summer all adult birds banded in Otago were resighted only in Otago, which indicates a high degree of philopatry. In contrast, a third of nestlings banded at Wairau were resighted as adults in the Otago area, indicating a southward natal dispersal. The annual survival rate is estimated to be 0.89 and 0.92 for Otago and Wairau birds, respectively. The oldest bird seen alive was 18 years and 3 months.

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INTRODUCTION

The royal spoonbill (*Platalea regia*) occurs throughout eastern and northern Australia, both main islands of New Zealand, and as vagrants in New Guinea and some of the Pacific islands. The successful natural colonisation of New Zealand by royal spoonbills has occurred since the 1950s. Although small numbers of vagrants were recorded in New Zealand from the mid-19th century (Heather & Robertson 1996), the first breeding colony was not discovered until 1949 at Okarito. Numbers of spoonbills remained low for decades (a count of 49

in a nationwide census in 1977; Heather 1978) but from 1990 numbers have increased markedly from 240 to 2300 in 2012 (Schweigman & Thompson 2012). This increase has been paralleled by an increase in the establishment of new breeding colonies, with the first colony outside Okarito found at Wairau lagoons in the 1979/1980 breeding season when 3 chicks successfully fledged (Holdaway 1980). Subsequently, colonies became established in Otago in 1984, expanding to 12 colonies by 2005 (Schweigman 2006). It is likely that the increase in population and geographic spread across New Zealand results from successful local breeding, but further influxes of Australian birds cannot be ruled out.

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Little is known about the movements of royal spoonbills and their annual survival is unstudied (Marchant & Higgins 1990). The New Zealand population presented an opportunity to study these aspects. Royal spoonbills are resident at their breeding grounds from late spring to late summer, but only a few are present during winter (Schweigman & Thompson 2012). Sightings in the winter at various estuaries around New Zealand suggested widespread post-breeding dispersal. A banding study was instigated to determine survival rates, movement patterns, and any differences in movements between juveniles and adults. We studied 2 breeding populations (Wairau and Otago) and report here the findings from a 20-year record of resightings of royal spoonbills banded as nestlings.

METHODS

The locations of the breeding colonies were on Green Island, Otago (45°57' S, 170°23' E) and in islands in the Wairau lagoon, Marlborough (41°32' S, 174°04' E) (Fig. 1a). The birds were banded as nestlings when aged between 3 and 6 weeks. Each bird was marked with a unique combination of 3 to 4 colour plastic bands (1 to 2 on each tibia) and a metal numbered band. Banding permits for this study were issued by the Department of Conservation. A total of 60 nestlings were banded by P.S. and his team at colonies at Green Island; between 3-13 chicks were banded in each of 10 seasons between 1994 and 2005 (mean = 5.7 per year). Ninety-eight chicks were banded by W.F.C. and his team at colonies at Wairau Lagoons; between 1 and 24 chicks (mean = 9.8 per year) were banded in 10 seasons between 1989/1990 and 2005/2006 (none were banded in seasons between 1997/98 and 2002/2003).

Requests for resightings were publicised via OSNZ publications and member networks, including Southern Bird. Observations were made by amateur and professional ornithologist throughout New Zealand, although it was not possible to ensure even coverage or observer effort. Observer effort was known to be low at the Wairau lagoons due to difficulty of access (8 observations in 20 years). Observers used binoculars and spotting scopes to read colour combinations of any banded spoonbills in flocks throughout the country. Resightings were collated by P.S. and W.F.C., and the database was maintained by the Department of Conservation Banding Office.

Resighting records from 1991 to 2012 were obtained from the Banding Office for analysis. There were 1358 resighting records, of which 737 were classified as independent resightings. Resightings were considered independent if they occurred in different locations, months or years. Multiple resightings of individual birds seen on

consecutive days at one location were classified as one independent resighting. Only independent resighting data were used in our analyses. Resightings of Otago and Wairau birds were analysed separately. Resightings were grouped into 4 seasonal periods: winter (June, July, August), spring (September, October), summer/breeding (November through February), and autumn (March, April, May). At each location for each season the resightings were further analysed by the calendar year since banding (age of bird).

The age of birds was defined by the following criteria: Y0, < 1 year since banding, first year of life; Y1, < 2 years since banding, in second year of life; Y2, < 3 years since banding, in third year of life; Y3, in fourth year of life; Y4, and so on. Y0 birds were considered juveniles, Y1 birds immatures and adults as Y2 and older.

Determination of annual survival rate

Annual survival was estimated by the Cormack-Jolly-Seber method (Lebreton *et al.* 1992), pooling all age classes and using all resightings of individual birds for each year from the start of banding until 2013, regardless of location. Models were considered in which resighting probability and survival rate varied annually or were constrained to a constant value across years. Analyses were performed using program DENSITY 5.0 (Efford 2012). Using Akaike's Information Criterion to compare models, the best model for both banding areas, by a large margin, was one with constant survival rate and varying resighting probability ($\Delta AIC > 26$). Estimates are reported from only this model, with 95% confidence intervals obtained by back transforming limits from the logit scale.

RESULTS

Resighting records

The total number of birds banded was 158 between 1989 and 2005. There were 170 independent resightings of Otago birds, only 2 of which were dead recoveries of juvenile birds (age 6 months and 8 months, respectively). There were 567 independent resightings of Wairau birds; 6 were dead recoveries (2 juveniles of 5 months and 9 months, and 4 adults). Seventy five percent of Otago birds (45 individuals) and 84% of Wairau birds (82 individuals) were resighted. Sixty one percent of Otago the birds and 74% of Wairau birds were resighted multiple times (>2 times), with 10% and 28% resighted more than 10 times, respectively.

The number of independent resightings were analysed by the age at which they occurred (Table 1). The number of resightings decreased with the age of the bird (years from banding) as would be expected. Most of the resightings were in the first

Table 1. Resightings of banded royal spoonbills in New Zealand. The number of resightings were grouped by the age of the bird since banding. The number of resightings for birds banded in Otago and Wairau are given, with percentage of total number of resightings in parentheses. *, includes 20 resightings of juveniles near natal site within 1–2 months after fledging.

Age at resighting	Number of resightings (% resightings)	
	Otago birds	Wairau birds
Y0	50* (29)	98 (17)
Y1	22 (13)	129 (23)
Y2	20 (12)	99 (17)
Y3	20 (12)	66 (12)
Y4	11 (6)	51 (9)
Y5	13 (8)	28 (5)
Y6	11 (6)	21 (4)
Y>6	23 (14)	75 (13)

5 years of life (72% and 78% for Otago and Wairau birds, respectively).

There were 30 resightings of 19 Otago juveniles away from the natal area and 20 resightings near the banding site of 12 recently fledged juveniles between 1–2 months old, which had not yet left the area. All resightings of Y1 birds were away from natal area. For Wairau birds, all resightings were away from the banding area and 56 birds were seen in the first year away from their natal area.

The locations of resightings are shown in Fig. 1. Birds from both Wairau and Otago were seen at the same locations, except only a Wairau bird was seen at Okarito. The furthest north destination was Parengarenga, 1280 km from Otago and 790 km from Wairau in a straight line.

The percent resightings of banded birds in winter at 8 different northern locations correlated significantly (correlation coefficient $r = 0.977$, $P < 0.01$) with the winter count of the number of birds at those locations as obtained from the 2012 winter census (Schweigman & Thompson 2012).

Seasonal resightings

The seasonal resightings were analysed by determining the number of resightings at each location in each season (Tables 2 and 3). The number of resightings in each season was also analysed by the age of the bird since banding. In Otago there were no resightings of banded birds of any age in April through October. Adult banded birds were resighted in Otago in all months from November through March (there was insufficient data for a similar analysis of Wairau birds). Adult banded birds were seen in the far north in all months from

April through October. There was a reciprocal shift in location for both Otago and Wairau birds from the north in winter to southern locations in summer and north again for winter.

Winter resightings

In winter essentially all birds moved from their southern natal and banding site to northern locations in winter (Table 2 and 3). In winter, 80% ($n = 40$) and 85% ($n = 176$) of all resightings of Otago and Wairau birds, respectively, were north of Kawhia. The highest number of resightings in the far north (Parengarenga and Rangaunu) were in the winter and birds of all ages were seen.

Juvenile Otago birds moved as far north as adults and there was no discernible difference in pattern of movement to the north in winter for juveniles and adults banded in Otago; about 80% of juveniles and immatures (Y0 and Y1) were seen in the north and about 80% of adults (>Y2) were seen in the north (Fig. 2a). There were only a few resightings in the central region and no Y0 juveniles from Otago were seen in the Nelson region.

For birds banded at Wairau, both juveniles and adults moved northwards in winter (Fig. 3a). However, there was a progressive shift to move further north with age; 31% ($n = 35$) of juveniles were seen in winter in the Nelson region, which is less than 100 km from the natal site, and the remainder in the far north (most at Parengarenga), and by Y1 only 12% ($n = 43$) of immatures were seen in the Nelson region with 84% in the far north (Fig. 3a). No banded birds were seen at locations south of the breeding site in winter.

Summer resightings

In summer, 84% ($n = 55$) resightings of Otago birds were in Otago (Table 2) and the small number seen elsewhere were juveniles and immatures and mainly seen at Mangere. In summer all resightings of juveniles and immatures (Y0, Y1) were in the northern and central regions with none resighted in the south (Fig. 2b). In summer, all adult banded birds were seen only in Otago (Fig. 2b).

Fifty four percent ($n = 111$) of all summer resightings of Wairau birds were also in Otago (Table 3). Eighty four percent ($n = 19$) of summer resightings in the north involved juveniles or immatures (Y0, Y1), and 80% ($n = 16$) of these were seen at Mangere.

The summer location of both Otago and Wairau birds shifted southwards as the birds got older (Fig 2b and 3b). For Otago birds only juveniles and immatures were seen in northern and central locations in summer whereas adult birds were only seen in Otago. For Wairau birds, juvenile and immature were also only seen in the north, whereas adult birds were also seen in central locations, mainly at their natal site at Wairau, as well as in the southern breeding locations.

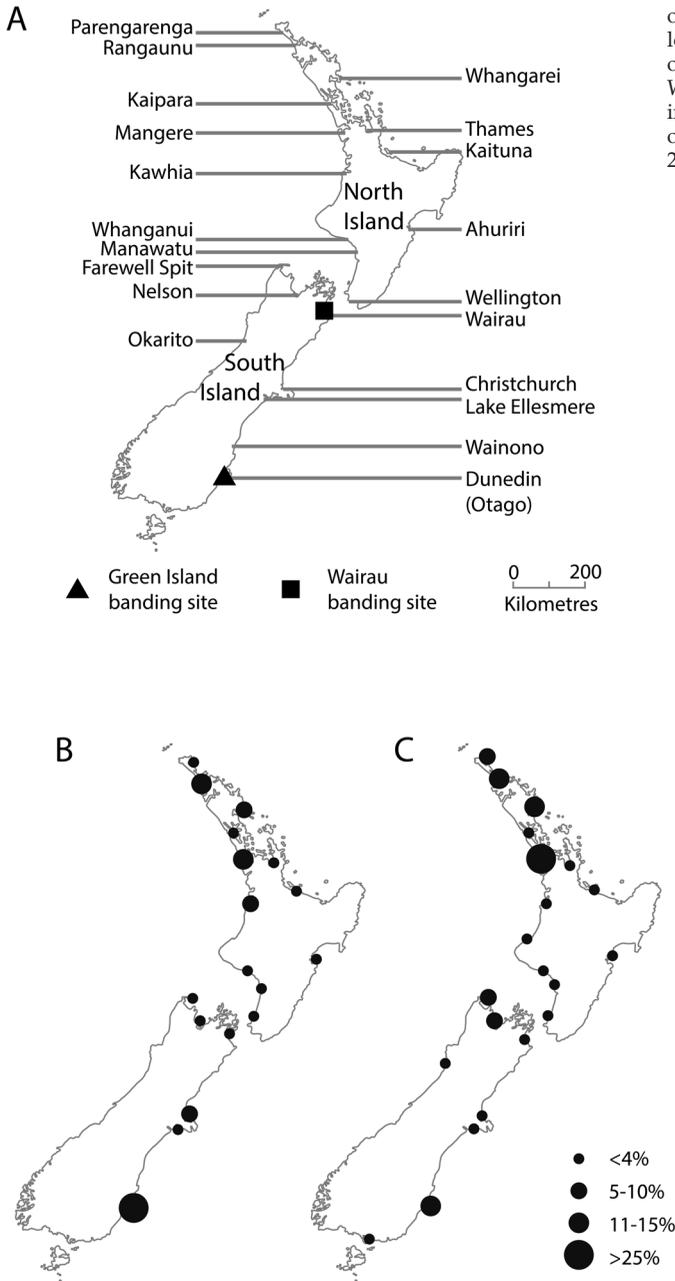


Fig. 1. Maps of New Zealand showing locations of resightings of royal spoonbills. A, names of locations referred to in the text. The locations of resightings of birds banded in Otago (B) and Wairau (C) with the percent of all resightings indicated by the size of the circles. The number of resightings at each location is given in Tables 2 and 3.

Autumn and spring resightings

In autumn there was an increase in the number of resightings in central locations (Nelson, Manawatu, Whanganui, Ahuriri) compared with summer. This was most clear for resightings of Wairau birds (Table 3); 56% ($n = 97$) of resightings at these central locations was in autumn and birds of all ages were seen. There

was also an increase in the number of resightings in the Christchurch region in autumn (Table 2 and 3). The highest percentage of resightings of Otago birds at Mangere was in autumn (Table 2), and the highest percentage of resightings of Wairau birds at Mangere was in spring (Table 3); 70% ($n = 163$) of all resightings at Mangere was in spring and autumn.

Table 2. Seasonal resightings at each location of birds banded at Otago. For each location the number of resightings are given for each season, with the percentage of all resightings that season in parentheses. The locations are listed from most northern (top) to most southern. Mangere: includes Mangere sewage ponds and other areas in the Manakau Harbour.

	Winter	Spring	Summer	Autumn	Total at each location	Percent at each location
Parengarenga	1 (3)	1 (6)	0	0	2	1
Rangaunu	13 (33)	3 (18)	0	3 (5)	19	11
Whangarei	6 (15)	1 (6)	0	8 (14)	15	9
Kaipara	1 (3)	0	0	2 (3)	3	2
Mangere	5 (13)	4 (24)	3 (5)	11 (19)	23	14
Thames/Kaituna	2 (5)	3 (18)	0	0	5	3
Kawhia	4 (10)	1 (6)	1 (2)	4 (7)	10	6
Whanganui	0	0	1 (2)	1 (2)	2	1
Manawatu	0	0	0	2 (3)	2	1
Ahuriri	0	0	0	1 (2)	1	1
Wellington	0	0	1 (2)	0	1	1
Farewell Spit	2 (5)	1 (6)	0	0	3	2
Nelson	3 (8)	1 (6)	0	0	4	2
Wairau	1 (3)	0	0	0	1	1
Christchurch	2 (5)	2 (12)	1 (2)	6 (10)	11	6
Lake Ellesmere	0	0	2 (4)	3 (5)	5	3
Otago	0	0	46 (84)	17 (29)	63	37
Southland	0	0	0	0	0	0
Total number of sightings	40	17	55	58	170	
Percent resightings each season	24	10	32	34		

Resightings in the Otago region

The number of birds resighted in Otago estuaries was grouped by age (years since banding; Table 4). All resightings of Otago birds were in summer and autumn (*i.e.*, presumed late leavers). All adult Otago birds (>Y2) were resighted only in Otago. Twenty six individual birds (57% of all resighted Otago birds) were resighted as adults back in their natal area, presumably breeding. Adult banded birds were resighted returning to Otago by 1 November.

All resightings of juvenile Otago birds (Y0) were within 14 km of their natal site, 1 – 2 months after fledging but before they left for northern locations. No juvenile birds were resighted in their natal area at the end of their first year (12 months after fledging; Table 4). The first birds to be resighted back in Otago were at the start of their third year of life (in January 2 years after banding).

Interestingly, 33 birds banded at Wairau (40% of all resighted birds) were resighted in estuaries around Dunedin. Most resightings (78%, $n = 77$) were in summer and the remainder in autumn

(presumed late leavers) and spring (earlier arrivals). Thirteen birds were seen in consecutive summers. The majority (93%, $n = 60$) of these resightings were of adults (>Y2), although 4 birds were seen during their second season after fledging (Table 4).

Movements of individual birds

Multiple resightings of individual birds tracked their seasonal movement patterns and confirmed the pattern derived from the analysis of independent resighting data (Table 2 and 3).

Some adult birds were seen at 3 locations in the same or consecutive years in the south and north and en route at Manawatu (4 examples), Mangere (6 examples), and Nelson (2 examples). One juvenile was seen at Lake Wairarapa en route to Mangere.

There were 20 examples of adult birds that were seen in the north in the winter and the again in the South Island (at breeding site) the following summer. Eleven examples were the same birds returning back north again the following winter to the same location.

Table 3. Seasonal resightings at each location of birds banded at Wairau. For each location the number of resightings are given for each season, with the percentage of all resightings that season in parentheses. The locations are listed from most northern (top) to most southern. Mangere: includes Mangere sewage ponds and other areas in the Manakau Harbour.

	Winter	Spring	Summer	Autumn	Total at each location	Percent at each location
Cape Reinga	0	0	0	1 (1)	1	0
Parengarenga	35 (20)	3 (3)	1 (1)	2 (1)	41	7
Rangaunu	52 (30)	7 (7)	1 (1)	22 (12)	82	14
Whangarei	29 (16)	7 (7)	1 (1)	24 (13)	61	11
Kaipara	0	0	0	2 (1)	2	0
Mangere	26 (15)	61 (61)	14 (13)	39 (22)	140	25
Thames/Kaituna	2 (1)	0	1 (1)	1 (1)	4	1
Kawhia	5 (3)	1 (1)	1 (1)	2 (1)	9	2
Taranaki	0	0	1 (1)	2 (1)	3	1
Whanganui	1 (1)	0	1 (1)	4 (2)	6	1
Manawatu	3 (2)	0	0	10 (6)	13	2
Ahuriri/Wairoa	2 (1)	0	0	10 (6)	12	2
Wellington	0	1 (1)	1 (1)	1 (1)	3	1
Farewell Spit	12 (7)	5 (5)	0	11 (11)	28	5
Nelson	8 (5)	4 (4)	4 (4)	16 (9)	32	6
Wairau	0	0	10 (9)	0	10	2
Okarito	0	1 (1)	1 (1)	0	2	0
Christchurch	1 (1)	0	6 (5)	8 (4)	15	3
Lake Ellesmere	0	0	5 (5)	12 (7)	17	3
Otago	0	7 (7)	60 (54)	10 (6)	77	14
Southland	0	3 (3)	3 (3)	3 (2)	9	2
Total number of resightings	176	100	111	180	567	
Percent resightings each season	31	18	19	32		

Some birds were seen on multiple occasions at the same winter and summer sites for many consecutive years. Three examples are given here:

(a) One Y1 bird from Wairau was seen at Lake Ellesmere in autumn (10 April 1992) and at Rangaunu in winter (20 June 1992) and was heading back down via Mangere in spring (11 to 26 October 1992) to Avon, Christchurch, by November (4 November 1992) and back to Rangaunu the following winter (13 May 1993), then south to Mangere (2 September 1993) and at Lake Ellesmere the following summer (10 April 1994) and back at Rangaunu by April (29 April 1994) for the winter (3 July 1994).

(b) Another bird banded at Wairau was seen on multiple consecutive occasions for 5 years. Two months after banding it was seen at the Manawatu

estuary (19 April 1992), then at Rangaunu by June (11 June 1992), back to Mangere (7 November 1992) then Ellesmere in summer and autumn (28 January 1993, 7 April 1993). It then moved back to Rangaunu in winter (4 August 1993), moving back down to Mangere in spring where it was seen multiple times (20 September 1993 to 29 October 1993), after which it was seen for the first time in the summer on Maukeikei Island off the coast of Otago (13 January 1994) at start of its third year. By 29 April 1994 it was back at Rangaunu and also seen there in winter (3 July 1994), then back at Mangere in spring (5 – 21 October 1994), en route to Kaikorai estuary, Otago, by 11 November 1994 for the summer (now mature and could breed). The following winter it moved back via Christchurch (8 April 1995) to Rangaunu (3 June 1995), back at Kaikorai

Fig. 2. Seasonal location of resightings of banded Otago birds by age. The winter (A) and summer (B) resightings were grouped by the age of the bird (years since banding: Y0, Y1, Y2 and >Y3) at resighting, and expressed as percentage of all resightings at that age for the locations as follows: white bar, northern, > 1000 km north of natal site (Kawhia to Parengarenga); grey bar, central, 400 – 800 km north of natal site (Christchurch to Whanganui); black bar, southern, < 400 km from natal site (Otago). The number of resightings (*n*) at each age is given in parentheses.

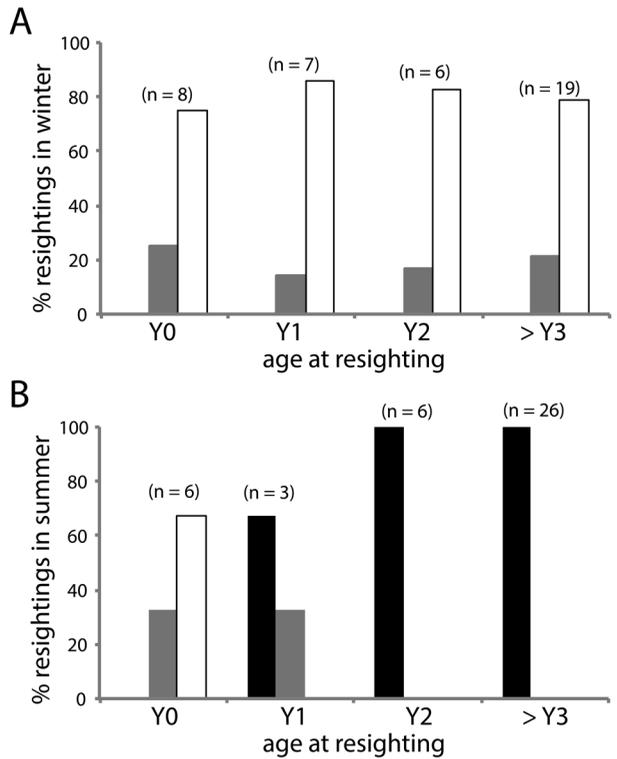
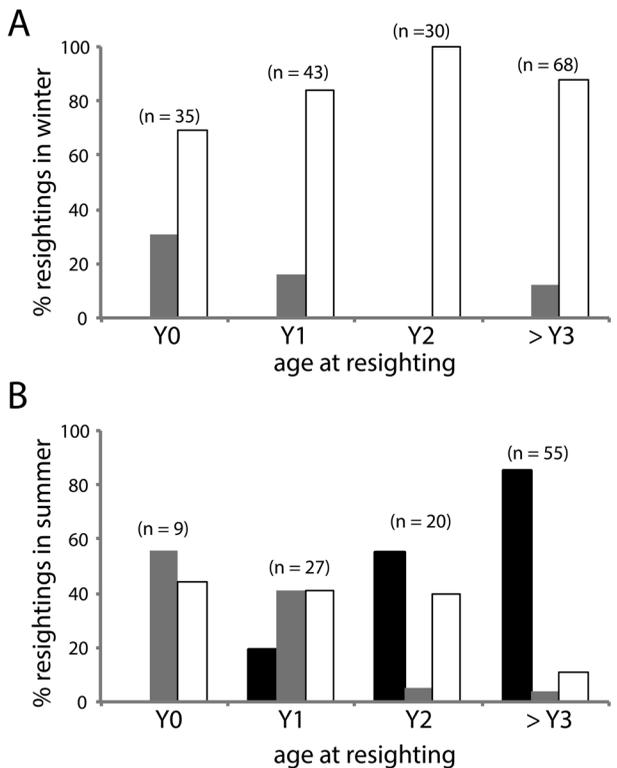


Fig. 3. Seasonal location of resightings of banded Wairau birds by age. The winter (A) and summer (B) resightings were grouped by the age of the bird (years since banding: Y0, Y1, Y2 and >Y3) at resighting, and expressed as percentage of all resightings at that age for the locations as follows: white bar, northern, 500 - 800 km north of natal site (Kawhia to Parengarenga); grey bar, central, < 400 km from natal site (Lake Ellesmere to Taranaki); black bar, southern, 500 - 800 km south of natal site (Otago and Southland). The number of resightings at each age is given in parentheses.



the following summer (6 November 1995 to 3 January 1996), back at Rangaunu in winter (10 June 1996), then Kaikorai the next summer (12 November 1996) and back at Rangaunu in winter (9 August 1997), now in its sixth year.

(c) Another bird banded at Wairau was seen on multiple occasions for 9 years. It was at Farewell Spit 4 months after fledging (5 May 1993) and then moved southwards to Okarito (5 October 1993) in its juvenile year. In autumn of Y1 it was back in the Nelson region and last seen there 23 June 1994, then less than 1 month later at Parengarenga on 03 July 1994, then south at Mangere in spring (16 November 1994). It was seen again at Okarito in the summer of the following year (5 December 1995). It was seen at Otago in the summer in Y6 and subsequently in Y7, Y8 and Y9.

Partial southward summer movements of juveniles and immatures

There were 13 examples (8% of banded birds) of juvenile and immature birds (Y0, Y1) appearing to attempt a partial southward movement in summer. Five birds moved south in summer to the Christchurch region at the start of their second year (2 from Rangaunu and 3 from Nelson region). Three birds moved from northern locations to Waikanae, Whanganui and Auckland in summer. Two birds moved south from northern locations before the end of winter to Whanganui (July) and Farewell Spit (August). One bird moved from summer at Miranda to winter at Kaituna, Bay of Plenty, then to Taupo (October).

Transit times

Determination of transit times is dependent on whether an observer is in the field to record departures and arrivals, so resightings can be only used to estimate minimum transit times. There were 10 records of birds seen within 1 month at 2 distant locations, giving transit times between 50 – 150 km/day. The fastest minimum transit time northwards was for a Y3 bird seen at Hawksbury lagoon, Otago, then 8 days later at Mangere sewage ponds, 1042 km away, giving 130 km/day. The fastest southward transit was by Y4 bird from Manakau to Wainono lagoon, Otago, 939 km away in 6 days, giving 156 km/day. Similar transit times were found for shorter distances: from Whangarei to Manakau (132 km) in 1 day by a Y0 bird, and from Manakau to Rangaunu, 267 km in 2 days by a Y2 bird.

Survival and longevity

Analyses of the resightings of individual birds each year estimated an annual survival rate for Otago birds of 0.89 (95% confidence interval: 0.85 to 0.92) and for Wairau birds of 0.92 (95% confidence

Table 4. Resightings in Otago region. The total number of resightings in Otago estuaries (near summer breeding sites) were grouped by the age of the bird (years since banding) at resighting, for birds banded at Otago and Wairau. The number of individual birds resighted is also given.

Year since banding	Number of resightings	
	Otago birds	Wairau birds
Y0	20	0
Y1	0	5
Y2	8	10
Y3	7	14
Y4	4	7
Y5	4	2
Y6	4	6
>Y6	16	33
Total number of resightings	63	77
Total number of birds resighted	26	33

interval: 0.90 to 0.94). Forty-three birds older than 8 years were resighted and of these 6 were older than 15 years. The longest period between banding and resighting for Otago bird was 15 years and 30 days (banded 17 December 1998 resighted 16 January 2014) and for a Wairau bird 18 years and 84 days (banded 24 January 1995 resighted 18 April 2013).

DISCUSSION

Seasonal movements

The pattern of seasonal movement was determined from the resightings of individually marked birds in different seasons at various locations throughout New Zealand, and the tracking of individual birds over time.

Our study is the first to show that adult royal spoonbills in New Zealand undertake repeated seasonal movements between summer locations at breeding sites in the South Island to spend the winter at locations in the North Island and back again the following summer to breeding sites in the south. Some birds travelled at least 1200 km, or further if they followed coastlines. Banded adults were seen in northern locations from May to September and in the Otago breeding area from November to March. Evidence of site fidelity comes from individual birds being seen year after year in the same winter and summer locations. Once established in adults these movements are not random dispersals but should be classed as true migration.

The main wintering grounds are in the far north, at Parengarenga, Rangaunu and Whangarei. This is a change from 30 years ago when Nelson and Manawatu were recognised as main wintering grounds (Heather 1978; Robertson & Reece 1980). Most of the summer breeding sites are now on the eastern coast of the South Island (Schweigman 2006) compared with only one site at Okarito prior to 1980.

Migration route

It would be expected that migrating spoonbills would stop over at estuaries en route as the minimum transit rate observed was 150 km/day. This study has provided some evidence of the route of movement. The resightings in locations midway between south and north (Manawatu, Whanganui, Ahuriri) are highest in spring and autumn when birds would be en route. In addition, the number of resightings at these central locations is very low, which is consistent with stop-overs of short duration so that birds were not resident long enough to be observed (or with low observer effort). Some individual birds tracked via central locations en route to northern or southern locations in same year made stop-offs at Lake Ellesmere (from Otago), Nelson, Manawatu or Mangere. This is consistent with birds moving north via Lake Ellesmere, and either along the west coast via Manawatu or the east coast via Ahuriri and stopping off at Mangere before heading further north. The single birds seen at Lake Wairarapa and Taupo provide insufficient evidence to support an inland path as a main route of movement.

Movement of juveniles

The majority of juveniles in their first migration moved as far north as adults. About a third of juveniles from Wairau overwintered in the Nelson region, which is only 100 km from their natal site, before moving to more northern locations when older. This contrasts with Otago juveniles, which were not seen in the Nelson region. Juveniles remain in the northern locations for up to 2 years and only, if at all, undertake partial southward movements in summer. Some juveniles were seen moving south again from a northern location before the end of winter. Mangere is a summer location for some juveniles and immatures. The first years of life appear to be an explorative period with the seasonal movement patterns seen in adults not yet established.

Juveniles move south to potential breeding sites during their second summer (end of second year/beginning of third year), but probably do not breed that season. First breeding for royal spoonbills in New Zealand has been observed at 3 years of age (Schweigman 1999).

Return to natal site

Nestlings banded at the Otago colony returned as adults to Otago estuaries near their natal site. These individual birds accounted for 57% of the resighted banded Otago birds. In summer, all adult birds (of those banded in Otago) were resighted only in Otago, which indicates a considerable degree of philopatry. It is presumed that these birds were breeding, but not necessarily at their exact natal site as there are now several colonies in close proximity. This has been directly confirmed for 2 birds that were observed nesting on nearby Taieri Island (17 km from their natal colony on Green Island; Schweigman 1999).

The proportion of chicks banded at Wairau that returned to their natal site could not be determined because there were insufficient observations at the Wairau breeding site. However, 5 birds fledged from the Wairau colonies were seen back at Wairau as adults, which suggests they do return to their natal site. But of particular note, over a third of birds that were banded at Wairau were resighted in summer as adults in Otago, and also some at Lake Ellesmere and in Southland. This indicates that the birds from Wairau are not entirely faithful to their natal site.

It is clear that adult birds from the Wairau population are extending their range southwards. They are presumably breeding at these new locations (Otago birds are also probably breeding elsewhere but this could not be determined from our data). This flexibility in breeding location could contribute to the observed expansion of the number of breeding colonies (Schweigman 2006). New colonies could be established by newly mature birds discovering new breeding sites. In addition, Wairau birds would encounter Otago birds at the northern wintering sites and could accompany them on their southward movement. Tracking of individual birds showed one from Wairau ended up at Lake Ellesmere and another at Otago, first as immatures and then as adults. They subsequently became faithful to new their breeding sites in Otago. The observation of one bird moving to Okarito suggests a link of Wairau birds with Okarito and perhaps the initial formation of the original colony at Wairau (Holdaway 1980); interestingly this bird eventually ended up in Otago, presumably breeding there.

Comparisons with other spoonbills

It is interesting that the New Zealand population of royal spoonbills, which would have originated from vagrant Australian birds, is behaving differently from most Australian populations. Australian populations of royal spoonbills are not known to undertake regular or pronounced long-distance movements (Marchant & Higgins 1990).

Spoonbills in most coastal sites are sedentary (Lowe 1982) and no seasonal trends in reporting rates have been noted (Marchant & Higgins 1990). Inland populations are considered nomadic because their movements fluctuate with changes in food supply and rainfall to areas with conditions suitable for breeding and foraging (Morton *et al.* 1993; Vestjens 1975). However, seasonal migration with return to natal sites as seen for royal spoonbills in New Zealand is also seen for 2 northern hemisphere species that have been studied. The black-faced spoonbill (*P. minor*; Ueta *et al.* 2002) and the Eurasian spoonbill (*P. leucorodia*; de le Court & Aguilera 1997; Lok *et al.* 2011) exhibit seasonal migration patterns reciprocal to those seen for our royal spoonbills, with regular return movements each year between northern breeding sites and southern wintering grounds up to several thousand km away.

It is interesting to consider how the New Zealand population of royal spoonbills developed seasonal movement patterns, especially as such migrations do not seem to occur in Australian populations. Migration is likely to have a genetic component and is assumed to develop to allow exploitation of highly productive breeding areas and benign wintering areas (Newton 2010). Royal spoonbills that arrived in New Zealand may be individuals with a genetic propensity for long-distance travel. For royal spoonbill in New Zealand, the question is in what ways do climatic conditions and food supply in the southern breeding sites in winter provide sufficient consistent selection pressure to drive seasonal migration so that the costs of moving north would be outweighed by benefits of wintering in the north, and vice versa.

Observer effort

Studies such as the present one have the inherent problem of bias in observer efforts between locations. Resightings may be higher in some locations and seasons simply due to presence of more active observers and lower in others due to fewer observers, generating unavoidable bias in the data. However, the resighting rate (75% and 84% for Otago and Wairau bird, respectively) was high, which suggests that there was good coverage of estuaries where birds were present, despite the possibility of uneven sampling effort. This is also supported by the high correlation of winter resightings with the total count of spoonbills in the winter census. There were fewer resightings in spring, which could be due to less observer effort, but it is more likely that in spring the birds may be more mobile and stay in one location for shorter durations before moving on so are less likely to be observed. In summer there were fewer resightings for Wairau birds and this is because there was low

observer effort at the Wairau location so any banded birds returning to their natal area would not have been observed. This meant that no firm conclusions about movements to and from the Wairau breeding site could be made.

Survival and longevity

Royal spoonbills are long-lived birds. This is the first report of annual survival rates for royal spoonbill. The annual survival rate was similar for Otago (0.89) and Wairau birds (0.92). The rate is higher than that determined for the Eurasian spoonbill (0.73, 0.83; Bauchau *et al.* 1998; Lok *et al.* 2011). The oldest royal spoonbill seen alive so far is 18 years and 3 months, which is lower than the Eurasian spoonbill, 28 years (Cramp 1994), but higher than either the black-faced, 9.5 years (Yu 2005) or roseate spoonbill, 15.8 years (USGS 2014).

It is not known whether the survival rate of Australian populations of royal spoonbills would be the same as for the New Zealand population. It may be that establishment of seasonal movements has been a strategy that has contributed to their high annual survival and the growth of the population in New Zealand.

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