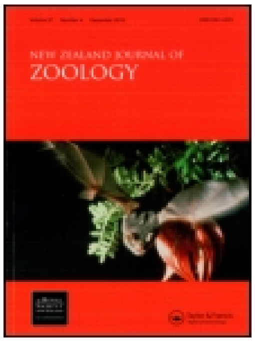

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The influence of age on laying date, clutch size, and egg size of the white-fronted tern, *Sterna striata*

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The age at first breeding and the influence of age on laying date, clutch size, and egg size of white-fronted terns were studied at the Kaikoura Peninsula, New Zealand, between 1971 and 1976. Of the 134 banded birds recovered breeding at Kaikoura, 63% were marked as nestlings at Kaikoura; the remainder came from colonies within 104 km. The bird is extremely capricious in its choice of nesting locality, and there are indications that it is not consistently philopatric. A small number bred as 3-year-olds, but the majority did not commence breeding until after they were 6 years old. Most pairs (73%) were of partners with an age difference of 1 year or less. Laying date and egg size varied with the age of the parent, but clutch size showed no significant change in relation to age. Mean egg volume did not vary between one-egg and two-egg clutches, but in two-egg clutches the first egg laid was significantly the larger in length, breadth, and volume. Single-egg clutches were the most common, but as the season progressed the proportion of two-egg clutches increased. There was no significant seasonal change in egg size.

Keywords: *Sterna striata*; breeding biology; age; banding; Kaikoura.

INTRODUCTION

The white-fronted tern, *Sterna striata*, breeds only in New Zealand and on some outlying islands (Falla *et al.* 1966). Colonies are usually situated at or near the coast, and the birds feed inshore on small fish. Studies of this medium-sized tern are confined to general accounts (e.g., Stead 1932, Oliver 1955) and a paper on dispersal (Clark & Dawson 1957). This paper describes the age at first breeding, and the effect of age on the timing of breeding, clutch size, and egg size.

In recent years a number of studies of long-lived seabirds have examined the effect of age on various aspects of breeding biology (e.g., yellow-eyed penguin, *Megadyptes antipodes* – Richdale 1955, 1957; kittiwake, *Rissa tridactyla* – Coulson & White 1958, 1960, Coulson 1963, 1966; red-billed gull, *Larus novaehollandiae scopulinus* – Mills 1973, 1979; fulmar, *Fulmarus glacialis* – Ollason & Dunnet 1978). However, published studies of this relationship among terns are confined to Austin (1945), Austin & Austin (1956), and Hays (1978) for the common tern, *Sterna hirundo*, and Coulson & Horobin (1976) for the Arctic tern, *S. paradisaea*.

The present study was carried out between 1971 and 1976 at the Kaikoura Peninsula (Fig. 1), where white-fronted terns nest in association with red-billed gulls. Nestlings have been banded at this locality and nearby almost annually since 1958.

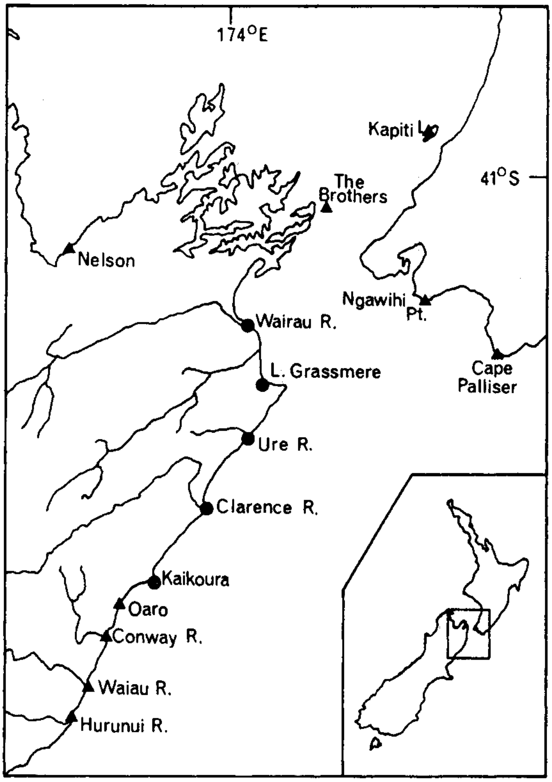

Fig. 1. Location of white-fronted tern colonies where chicks have been banded, 1958–74. Terns from marked sites were (●) recovered breeding or (△) not recovered breeding at Kaikoura.

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METHOD OF DATA COLLECTION AND ITS LIMITATIONS

Breeding adults were captured at the nest with an automatic drop trap (Mills & Ryder 1979) or a pole net. Trapping had to be confined to the period when small chicks were in the nest; if attempted when adults were incubating eggs it invariably led to desertion. The necessity for capturing birds when they had chicks may have resulted in young birds being under-represented in the sample of known-age terns, since in other studies it has been demonstrated that young birds tend to have a lower hatching success than older individuals (e.g., kittiwake – Coulson 1966; red-billed gull – Mills 1973; Arctic tern – Coulson & Horobin 1976). Thus, a disproportionate number of older birds may have been available for capture. The small numbers on the band and the corrosion and abrasion of its external surface precluded reading the band number using binoculars or a telescope.

None of the captured birds had bands showing signs of opening up and falling off, as has been found with the herring gull (Poulding 1954), ring-billed gull, *Larus delawarensis* (Ludwig 1967), and red-billed gull (Mills 1972), but excessive wear prevented identification of the band number on 12 (11%) of 107 banded terns captured in 1976–77. These unidentifiable birds probably belonged to older age groups, and so they too may be under-represented in the known-age sample.

In the 1971–72 and 1972–73 breeding seasons banded white-fronted terns were captured at Kaikoura for determination of the age at first breeding and the banding locality. In the 1976–77 breeding season the study was extended to investigate the effect of age on aspects of breeding biology. Two areas within a colony of *c.*1500 pairs on Sugarloaf Point, Kaikoura Peninsula, were chosen for study. In all, 180 nests were marked, and these were visited daily. When the date of laying was unknown it was determined by subtracting the incubation period (24 days) from the hatching date.

The birds were not sexed, so the contribution to breeding that each member of the pair made relative to its age could not be analysed. However, in most pairs the partners were of similar age (see Table 3), so this was taken as standard for analyses of the effect of age on clutch size, laying date, and egg size. The same assumption was made by Coulson & Horobin (1976) in their study of the effects of age on breeding in the Arctic tern.

RESULTS

Place of Origin of the Kaikoura Breeding Terns

White-fronted terns are characteristically capricious in their choice of nesting locality; a site used one year may not be used the next (Falla *et al.* 1966). This applied at Kaikoura, for although terns have nested there in most years since 1964, the numbers of pairs varied from about 20 to several thousand.

Table 1. Natal locality of banded white-fronted terns recovered breeding at Kaikoura Peninsula in 1971–72, 1972–73, and 1976–77 (percentage recovered in parentheses). NCB – no. of chicks banded; NRB – no. recovered breeding.

Year banded	*Kaikoura* NCB	*Kaikoura* NRB	*Clarence R. mouth* NCB	*Clarence R. mouth* NRB	*Ure R. mouth* NCB	*Ure R. mouth* NRB	*L. Grassmere* NCB	*L. Grassmere* NRB	*Wairau R. mouth* NCB	*Wairau R. mouth* NRB
1958–59	359	3(0.8)								
1959–60	580	21(3.6)								
1960–61	356	9(2.5)					108	0		
1961–62	487	19(3.9)	786	11(1.3)						
1962–63	713	24(3.3)			701	9(1.2)				
1963–64	57	1(1.7)	343	1(0.3)						
1964–65	19	1(5.2)							437	3(0.7)
1965–66	5	2(40.0)	1143	8(0.7)						
1966–67	8	1(12.5)	1450	11(0.8)						
1967–68										
1968–69							150	4(2.6)		
1969–70										
1970–71			950	2(0.2)						
1971–72	190	0			450	1(0.2)				
1972–73	58	0								
1973–74	800	3(0.4)								
1974–75	300	0								
1975–76	50	0								
Total*	**3632**	**84**(2.3)	**4672**	**33**(0.7)	**1151**	**10**(0.9)	**258**	**4**(1.6)	**437**	**3**(0.7)

*Excludes terns banded 2 years before recovery date, since these would not contribute to the breeding population.

Of the 134 banded white-fronted terns recovered breeding at Kaikoura Peninsula, 63% had been marked as nestlings at Kaikoura (Table 1). The next largest contingent (25%) originated from the Clarence River mouth, 33 km to the north; colonies from the Ure River mouth (65 km north), Lake Grassmere (86 km north), and Wairau River mouth (104 km north) contributed 7%, 3%, and 2% respectively of the banded birds (Table 1, Fig. 1).

The oldest terns recovered (18 years old) had been marked in 1958, the year banding commenced at Kaikoura. Since 1958 banding has also been carried out at Nelson, Cape Palliser, Ngawihi Point, Kapiti Island, The Brothers, the Conway River mouth, and the Hurunui River mouth (Fig. 1, Appendix), all within a radius of 200 km of Kaikoura, but no birds from these localities were recovered at Kaikoura.

The relatively high recovery rates of terns from the Clarence, Ure, Wairau, and Grassmere colonies (Table 1) indicates that the species is not very philopatric, or at least not consistently so. An example of its changeability as regards nesting locality is exhibited by a tern banded as a nestling at Kaikoura in November 1961 that was subsequently recovered breeding at the Clarence River mouth in 1965–66 and at Kaikoura in 1971–72 and 1977–78.

Age at First Breeding

The ages of banded white-fronted terns recovered breeding at Kaikoura are shown in Table 2. Only 4% were under 7 years of age. No 2-year-olds were recovered, and the youngest breeders were 3 years old (three individuals). As mentioned above, the youngest and the oldest age groups may be under-represented in the age structure. However, it is unlikely that the paucity of young birds in the known-age sample is due entirely to trapping bias, so it seems that the white-fronted tern has a long-deferred maturity, few birds commencing breeding under 7 years of age.

Age of Breeding Partners

In 1976–77 11 pairs of known age were captured (Table 3); the ages of the partners in 8 pairs were the same, or differed by only 1 year. The greatest age difference was 7 years, between a bird 17 years of age and its 10-year-old partner.

Mating of similar-age partners has been noted in other long-lived sea birds (e.g., yellow-eyed penguin – Richdale 1957; kittiwake – Coulson 1966; red-billed gull – Mills 1973; Arctic tern – Coulson & Horobin 1976; fulmar – Ollason & Dunnet 1978). This probably results from the tendency for birds of similar age to assume breeding condition at the same time. Because young birds tend to breed later in the season there is a greater likelihood of them mating together. Retention of pair-bonds from one season to the next would maintain the age similarity (Mills 1973).

Laying Date

Although egg-laying in the white-fronted tern is highly synchronised, there were differences in the timing of laying between age groups (Table 4). There was a trend for a progressive advance in

Table 2. Age structure of banded white-fronted terns recovered breeding at Kaikoura Peninsula. Banding totals refer to birds banded at localities from Conway R. mouth to Wairau R. mouth from 1958.

	Year Recovered							
	1971–72		1972–73		1976–77			
Age (years)	No. banded	No. recovered	No. banded	No. recovered	No. banded	No. recovered	Total banded	Total recovered
1	950		640		50		**1640**	
2	200		950		300		**1450**	
3	150		200		800	3	**1150**	**3**
4	0		150		58		**208**	
5	1458		0		640	1	**2098**	**1**
6	1148		1458		950	2	**3556**	**2**
7	456	1	1148	1	200		**1804**	**2**
8	514	3	456		150	4	**1120**	**7**
9	1414	5	514		0		**1928**	**5**
10	1273	6	1414	4	1458	12	**4145**	**22**
11	464	3	1273	6	1148	9	**2885**	**18**
12	580	7	464		456	3	**1500**	**10**
13	359		580	1	514	1	**1453**	**2**
14			359	2	1414	22	**1773**	**24**
15					1273	18	**1273**	**18**
16					464	6	**464**	**6**
17					580	13	**580**	**13**
18					359	1	**359**	**1**
Total		**25**		**14**		**95**		**134**

laying date with age for birds up to 11 years old. Birds in the 3–5-year age group bred on average 10.7 days later than those of the 12–14 age group ($0.05<P<0.1$), and the 10–11-year-olds bred on average 2.9 days earlier than the 12–14-year-old terns ($P<0.02$). There was no significant difference between the laying dates of the 12–14 and 15–18-year age groups.

Table 3. Age (years) of 11 pairs of white-fronted terns banded as chicks.

Elder partner	Younger partner	Elder partner	Younger partner
17	16	15	10
17	10	14	14
16	15	14	13
16	15	11	11
15	14	11	10
15	11		

Clutch Size

Of the 180 nests that were monitored, 81% contained a single egg and 19% had two-egg clutches. Three-egg clutches are known to occur occasionally at Kaikoura, but none were observed in the 1976–77 breeding season.

As the season progressed the clutch size increased (Table 5). A similar trend has been reported for the Sandwich tern, *Thalasseus sandvicensis* (Langham 1974), but for other terns—roseate (*Sterna dougallii*), common (*S. hirundo*), and Arctic (*S. paradisaea*) (Langham 1974)—a seasonal decrease has been recorded.

Table 6 shows the clutch sizes of known-age terns. Although there was a trend for increase in the percentage composition of two-egg clutches being laid between the 6–8-year and 12–14-year age groups, mean clutch size showed no significant differences.

Table 4. Effect of age on laying date, white-fronted tern.

Age group (years)	No. of birds	Mean laying date	S.D.
3–5	3	16.3 Nov	7.23
6–8	6	9.0 Nov	6.16
10–11	17	8.5 Nov	4.04
12–14	21	5.6 Nov	2.59
15–18	35	7.2 Nov	4.61

t_{25} (6–8 cf. 12–14 year cohorts) = 2.0406, P = 0.1–0.05
t_{36} (10–11 cf. 12–14 year cohorts) = 2.6057, $P<0.02$
t_{22} (3–5 cf. 12–14 year cohorts) = 5.2629, $P<0.001$

Table 5. Variation in clutch size and egg size according to laying date, white-fronted tern.

Laying date	Clutch size No.	Clutch size Mean	Clutch size S.D.	Egg volume (ml) No.	Egg volume (ml) Mean	Egg volume (ml) S.D.
30 Oct – 3 Nov	17	1.12	0.35	13	25.2	1.48
4 Nov – 8 Nov	68	1.19	0.39	62	24.7	1.64
9 Nov – 13 Nov	33	1.21	0.41	35	24.7	1.50
14 Nov – 24 Nov	9	1.66	0.50	15	24.9	1.73

t_{73} (30 Oct – 3 Nov cf. 4–8 Nov, egg volume) = 1.05, n.s.
t_{48} (30 Oct – 3 Nov cf. 9–13 Nov, clutch size) = 0.7708, n.s.
t_{40} (9–13 Nov cf. 14–24 Nov, clutch size) = 6.1913, $P<0.001$
t_{24} (30 Oct – 3 Nov cf. 14–24 Nov, clutch size) = 5.9719, $P<0.001$

Egg Size

Eggs were measured with vernier calipers to the nearest 0.1 mm, and egg volumes were computed from the relationship derived by Coulson (1963): volume (ml) = breadth^2 (mm) × length (mm) × 0.000478. There was no significant difference in mean egg volume between one-egg and two-egg clutches (Table 7), but in two-egg clutches the first egg laid was significantly the larger in length, breadth, and volume (Table 8).

In many seabirds (e.g., herring gull, *Larus argentatus* – Paludan 1951, Parsons 1970, 1972; kittiwake – Coulson 1963; the shag *Phalacrocorax aristotelis* – Coulson *et al.* 1969) it is common for eggs laid later in the season to be smaller. An analysis for this variation in the white-fronted tern (see Table 5) shows that eggs laid at the beginning of the breeding season had a slightly greater mean volume than those laid later, but the differences are not statistically significant.

Egg sizes of known-age white-fronted terns are shown in Table 9. Eggs laid by birds in the 3–5-year and 6–8-year age groups were significantly shorter than eggs laid by birds in the 12–14-year class, but

Table 6. Effect of age on clutch size, white-fronted tern (% composition of clutches in parentheses).

Age group (years)	No. of clutches	Clutch size 1	Clutch size 2	Mean clutch	S.D.
3–5	4	2 (50/50)	2	1.50	0.57
6–8	6	5 (83/17)	1	1.16	0.40
10–11	16	13 (81/19)	3	1.18	0.40
12–14	20	15 (75/25)	5	1.25	0.44
15–18	36	27 (75/25)	9	1.25	0.44

Table 7. Egg size in 1-egg and 2-egg clutches, white-fronted tern.

Clutch size	No. of clutches	Length (mm) Mean	Length (mm) S.D.	Breadth (mm) Mean	Breadth (mm) S.D.	Volume (ml) Mean	Volume (ml) S.D.
1	112	46.4	1.81	33.4	1.00	24.7	1.9
2	36	46.3	1.62	33.1	0.80	24.3	1.7

thereafter the difference was not significant. Egg breadth and egg volume increased between the 3–5-year and 6–8-year age groups, but there was no further increase with age.

DISCUSSION

In common with other long-lived seabirds, the white-fronted tern shows age-related variation in its breeding biology. Older terns bred earlier in the season and laid bigger eggs than younger individuals. These differences may be related directly to age and/or to breeding experience, both of which improve foraging and breeding efficiency. Plunge diving for fish requires skill, and the ability to frequently and rapidly capture the extra prey needed during the breeding season presumably could improve with age, as documented for other fish-eating species (e.g., Sandwich tern – Dunn 1972; brown pelican, *Pelecanus occidentalis* – Orians 1969; little blue heron, *Florida caerulea* – Recher & Recher 1969). Older, more experienced individuals would not only be more capable of supporting themselves and their offspring, but would be able to accumulate greater reserves, enabling them to breed earlier and to produce larger eggs than younger terns.

Differences in clutch size, laying date, and egg size between extreme age groups of the white-fronted tern were not as marked as in the red-billed gull (Mills 1973, 1979), which also nests at Kaikoura. These small differences may be related to the more synchronous laying of the tern. The red-billed gull's laying period can extend over 12 weeks, during which the abundance of euphausiids, their main food, changes (Bradford 1972). The large differences in aspects of the reproductive biology between extreme age groups of this gull may therefore result from the combined effect of changing food supply and the bird's ability to exploit the resource. The younger red-billed gulls, which tend to nest later in the season, are at a double disadvantage because they are presumably less efficient at foraging and are attempting to breed at a time when food is diminishing, so they produce smaller clutches and eggs. In contrast, the white-fronted tern has a laying period of only about 4 weeks, and it is reasonable to expect that the abundance of fish would not vary greatly over this shorter period. If this is so, then the differences in breeding biology between young and old terns would seem to be related to age or experience rather than to a change in food supply.

No consistent decrease in egg size, laying date, or clutch size occurred in the oldest age groups, so there is no evidence of 'senility'. For the yellow-eyed penguin (Richdale 1957), kittiwake (Coulson & White 1958), herring gull (Davis 1975), and red-billed gull (Mills 1979) there is a suggestion that older birds lay slightly smaller eggs.

Although the breeding age structure we obtained may be biased in favour of older individuals, because of the timing of capture, the pattern is similar to that obtained for other terns. The earliest confirmed breeding of a white-fronted tern was at age 3 years. Coulson & Horobin (1976), studying the Arctic tern, also failed to recover 2-year-olds breeding, and concluded that most birds commenced only when 4 years old. Similarly, for the common tern Austin & Austin (1956) found that less than 1% of the population bred as 2-year-olds, with the greatest proportion commencing at age 4 years; and for the sooty tern, *S. fuscata,* Harrington (1974) reported that the earliest breeding occurred at 3 years of age, though most individuals did not breed until 6–8 years old, and a few probably not until aged 10. Ollason & Dunnet (1978) point out that deferred maturity may allow birds to become sufficiently skilled at obtaining food to support themselves and their young, and as a consequence the age at first breeding probably balances the advantage of breeding while young, to increase the individual's total reproductive output, against the risk of increased mortality which may result from this.

In contrast to findings from other studies of populations of marked

Table 8. Egg size in 2-egg clutches according to laying sequence, white-fronted tern.

Position in clutch	n	Length (mm) Mean	S.D.	Breadth (mm) Mean	S.D.	Volume (ml) Mean	S.D.
Egg 1	34	46.9	1.52	33.4	0.73	24.9	1.65
Egg 2	34	45.7	1.61	32.8	0.76	23.6	1.50
Difference between means		$P<0.01$		$P<0.01$		$P<0.001$	

Table 9. Influence of age on egg size, white-fronted tern.

Age group (years)	No. of eggs	Length (mm) Mean	S.D.	Breadth (mm) Mean	S.D.	Volume (ml) Mean	S.D.
3–5	6	45.4	0.65	32.6	0.77	23.1	1.38
6–8	7	45.7	1.52	34.0	0.57	25.2	1.27
10–11	17	46.6	1.63	33.3	0.61	24.7	1.50
12–14	20	47.0	1.58	33.3	0.63	24.9	1.50
15–18	35	46.5	1.69	33.4	0.81	24.8	1.72

t_{25} (6–8 cf. 12–14 year cohorts; length) = 1.8905, P = 0.1–0.05
t_{24} (3–5 cf. 12–14 year cohorts; length) = 2.3924, $P<0.05$
t_{53} (12–14 cf. 15–18 year cohorts; length) = 1.0801, n.s.
t_{11} (3–5 cf. 6–8 year cohorts; breadth) = 3.7653, $P<0.01$
t_{11} (3–5 cf. 6–8 year cohorts; volume) = 2.8570, $P<0.02$

terns (e.g., common tern – Austin & Austin 1956; sooty tern – Harrington 1974; Arctic tern – Coulson & Horobin 1976) the white-fronted tern did not show a strong tendency to breed at the natal locality. This was reflected in the high proportion of the terns breeding at Kaikoura that were banded as nestlings elsewhere, and in the marked fluctuations in the numbers of adults nesting annually at Kaikoura.

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Appendix. Numbers of white-fronted terns banded as chicks at (a) 'mainland' New Zealand and (b) outlying island localities from 1958 to January 1977.

(a)	Ashley R. mouth	1
	Auckland	217
	The Brothers	328
	Clarence R. mouth	4672
	Clevedon	50
	Conway R. mouth	200
	Firth of Thames	240
	Haast R. mouth	28
	Hauraki Gulf	494
	Hurunui R. mouth	75
	Invercargill (estuary)	471
	Kaikoura	3982
	Kaipara Heads	3
	Kapiti I.	40
	Karitane Beach	9
	L. Ellesmere	463
	L. Grassmere	258
	Lyttelton	3
	Miranda	669
	Muriwai	5
	Napier	192
	Ngawihi Point	61
	Nelson	1323
	New Plymouth	202
	Okarito R. mouth	13
	Oaro	114
	Palliser Spit	125
	Sumner Heads	59
	Tutaekuri R. mouth	100
	Ure R. mouth	1151
	Waiheke I.	27
	Waipu R. mouth	80
	Wairau R. mouth	437
	Waitaki R. mouth	301
	Waitangi Beach, Clive	60
	Waituna Lagoon	329
		16 782
(b)	Auckland Is	7
	Chatham Is	160
		167