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## Reproductive Parameters, Chick Growth and Adult 'Age' in Australasian Gannets *Morus serrator* Breeding in Port Phillip Bay, Victoria, in 1994–95

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**Summary:** Reproductive parameters of Australasian Gannets *Morus serrator* breeding at Pope's Eye in Port Phillip Bay, Victoria, Australia were examined in the 1994–95 breeding period. Contents of individual nests were determined during routine visits, and eggs and chicks measured. Nests and breeding birds were assigned to groups based on position and adults of known age (previously banded as chicks) as indicators. A severe storm in November 1994 removed most nests and resulted in extensive re-laying, particularly by older (centrally nesting) birds. The ability to re-lay

and successfully raise young suggested that food (preferentially Pilchards *Sardinops sagax*, although gannets take a wide range of fish at this location) was not limiting, being abundant even towards later stages of the breeding cycle. 'Older' adults formed more central nests, laid earlier, and replaced more lost eggs than younger birds. Chicks of older adults were produced earlier and were heavier at comparable ages than those of younger birds. Age influences some reproductive parameters, and hence lifetime reproductive success, in this species as it does in other seabirds.

Earlier assumptions that reproductive success (and survival) is constant with increased age (e.g. Lack 1954) have been reconsidered. It is now recognised that life history strategies reflect various trade-offs between costs and benefits of reproduction, tending to optimise lifetime reproductive success (LRS, e.g. Newton 1989). Variations in reproductive success involve at least four major components: longevity, fecundity, mating success and offspring survival, and interactions between them (Clutton-Brock 1988; Stearns 1992). Some studies have shown relationships between increased age, breeding experience and reproductive success. For example, reproductive success (fledged young) in Short-tailed Shearwaters *Puffinus tenuirostris* increases with experience, plateaus and later declines. Mortality in that species is not constant: survival and output vary with experience, birds that live longer have a higher success, as do those that are older at first breeding (Wooller et al. 1988, 1989, 1990). While Dann & Cullen (1990) found that mortality increased with age (after four years) in Little Penguins *Eudyptula minor*, reproductive performance increased with breeding experience for at least four years. However, a more recent analysis (Dann et al. 1995) provided a more equivocal relationship between increased age and success. In other species too there is age-specific mortality, and age (and experience) can influence breeding success (e.g. Northern Fulmar

*Fulmarus glacialis*, Ollason & Dunnet 1983; Kittiwake *Rissa tridactyla*, Coulson 1966, Coulson & Wooller 1976; Blue-eyed Shags *Phalacrocorax atriceps*, Shaw 1995).

Feeding and breeding success in the Australasian Gannet *Morus serrator* (hereafter Gannet) may be inter-related and concurrently improve with age (as in the Brown Pelican *Pelecanus occidentalis*, Blus & Keahey 1978). Previous studies have not considered birds of known age. However, since age-specific survival and fecundity are significant in determining LRS, it is important to understand their influence in this species which is a major component of the local avian biomass (Norman 1992), with an increasing local breeding population (Norman et al. 1998). Since only single egg clutches are laid in this strongly philopatric species (Norman & Menkhurst 1995), LRS depends on successfully raising a chick to fledging (and beyond) rather than adjusting numbers of chicks fledged from a larger clutch. This study examined the influence of 'age' on some reproductive parameters at one of the few colonies readily accessible within the Australian range of the species. It allowed sampling of a mixed-age cohort of adults during a single breeding period; measurement of chick growth allowed some elaboration on the broader influence of time (date) and weather on breeding generally.

## Methods

### Study site

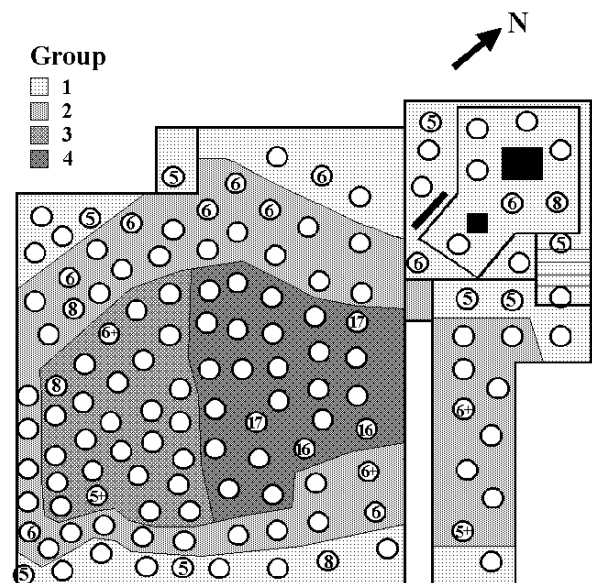
Pope's Eye (38°16'42"S, 144°41'48"E) lies about three km from Queenscliff, near the entrance to Port Phillip Bay, Victoria (see Norman & Menkhurst 1995). A wooden landing platform and an extension, concrete formations associated with a small tower and beacon, and a walkway (all c. 1.2–3 m above mean high water) have been erected on the artificial rock annulus and these provide the main nesting area for the colony where breeding was first recorded in 1985. Norman & Menkhurst (1995) detailed aspects of the site, colony growth and local weather conditions. The Pope's Eye colony developed, in part at least, from Gannets originally hatched at nearby Wedge Light, itself a relatively recent (1966) colony on another artificial structure (Norman & Menkhurst 1995). Previous studies showed that nest building begins in August–September, egg laying occurs mainly in September, hatching in October–November and most chicks fledge in January and February (Norman & Menkhurst 1995). Some variation occurs from year to year, and re-laid clutches can extend breeding periods. At this site, foods taken are mainly inshore schooling and pelagic species, particularly Pilchards *Sardinops sagax* (Norman & Menkhurst 1995). Of relevance here is the colony's accessibility, the presence of adults banded as chicks at Wedge Light (since 1967) or Pope's Eye (1986), and the exposure of this low-lying site to wave action. There were c. 120 nests present in 1991–92, and about 140 in the 1994–95 breeding period. Meteorological data for Point Lonsdale were provided by the Bureau of Meteorology.

### Parameters measured

Visits to the colony, influenced by weather, were made at approximately seven day intervals (range 4–10) from 26 July 1994 to 27 February 1995, and lasted 4–7 h. A visit was also made on 21 March to determine the fate of late chicks. Before egg-laying, landings were made on rocks near the wooden platforms to reduce disturbance. Later, when nests had also been formed on the rocks, platforms were used since birds then usually remained on nests with eggs.

Nests present at each visit were checked, and positions mapped using photographs and sketches. Once nest positions stabilised, they were grouped into 1, peripheral; 2, intermediate; and 3, central, on the platform added in 1989, and 4, central, on the old platform.

This grouping also reflected the distribution of known-aged adults (Fig. 1). Eggs were numbered using a permanent marker, and lengths, widths (to 0.1 mm, using dial calipers) and mass ( $\pm 2$  g, Pesola 300 g spring balance) determined. Egg volume ( $\text{length} \times \text{width}^2$ ) and shape ( $\text{width/length} \times 100$ ) indices were also determined (see Coulson 1963; Preston 1974; Brooke 1978). Chicks were weighed whenever possible (in small plastic or larger calico bags, depending on age, using Pesola (300 g) or Salter (2 kg, to 10 g, and 10 kg, to 50 g) balances) and measured (total head length, bill length and depth, using calipers (to 0.1 mm); flattened folded wing and tail length (1 mm, using stopped rules)). Daily rates of mass increase were calculated between visits and the midpoint used in analyses below: differences from the mean were used to examine changes in mass (mean relative mass) and wing length (mean relative length). Chicks were 'aged' at first measurement using wing length (Wingham 1984b) and banded as practicable when c. 40 days old. Egg laying, egg size, hatching and fledging, chick growth, and re-laying of lost clutches are considered generally, and for individual groups.



**Figure 1** Distribution of known-age adult Australasian Gannets, and nest groups established on the basis of adult age and nest site quality, Pope's Eye, Port Phillip Bay, 1994–95. Circles indicate occupied nests; numbers in circles show known or minimum (+) ages. Group 1 = young adults, peripheral sites; group 2 = intermediate age and quality; group 3 = older adults, central sites; group 4 = central sites, oldest adults.

Band numbers of attending or brooding gannets were obtained when possible, using binoculars or by gently lifting a sitting bird. Breeding birds earlier banded as chicks were assigned to a seasonal cohort, and recoveries (here, = found dead) of banded birds have been examined to indicate age of return to the colony area. Multivariate analyses were not applied here, since data were insufficient, but significance tests ( $P < 0.05$ ) have been conducted as planned comparisons, assuming unequal variances. General linear model (GLM) and Tukey studentised range analyses were conducted using SAS software (SAS 1987).

## Results

### Mortality, local recoveries and age of gannets at Pope's Eye

Between 1967 and 1981, 125 chicks were banded at Wedge Light; from 1986 to 1992, a further 92 were banded there and, between 1988 and 1992, 176 were banded at Pope's Eye. To 31 December 1996 there were 34 recoveries (8.6% of those banded at Pope's Eye or Wedge Light), and 28 of these were within Port Phillip Bay. About 41% (14) of recoveries occurred within six months of banding, four within 17–24 months, two within 26 months and six within 34–39 months after banding, and others later. Such details suggest that mortality is extensive immediately following fledging, that young are absent from the area for at least one breeding period, and subsequently return to colonies two or three years after fledging. Sightings of previously banded birds supported this. In this study, 82 banded birds were recorded. Breeding adults ranged from four to 18 years old; younger birds (2–3 years old) arrived late in the season and did not nest. The proportion of birds of known age found nesting increased from four (three of 12 nesting) to six (32 of 39) years old and all eight-year old birds recorded (seven) had nests. Approximately 24% of six-year old birds banded locally were seen at Pope's Eye during this study, as were three adults banded as chicks at Lawrence Rocks four (not breeding), six and eight years previously.

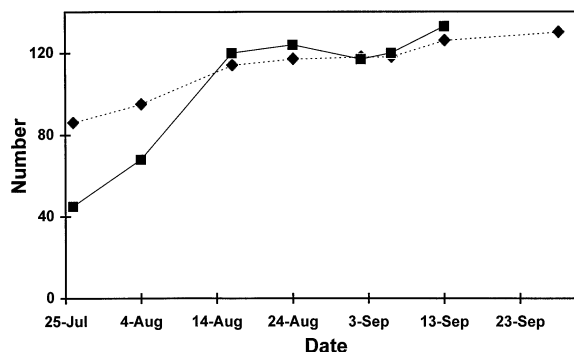
### Arrival, nest formation, density and location in relation to age

Nest building began before the first visit (26 July 1994); numbers of adult Gannets at the colony, and nests formed, increased gradually between late July and October (Fig. 2). Excluding those on rocks ( $< 0.5$

nests/m<sup>2</sup>), nest density averaged 1.6/m<sup>2</sup> ( $n = 132$ ) for the whole colony, being higher on the main platform (1.7/m<sup>2</sup>,  $n = 105$ ) than on the walkway (1.6,  $n = 14$ ) or tower (1.3,  $n = 13$ ).

The distribution of dates on which known-aged individuals were first recorded suggested a tendency for older birds to arrive earlier in the breeding period than younger birds ( $r = 0.245$ ,  $P = 0.02$ ,  $n = 68$ ), but exclusion of  $< 4$  year old (non-breeding) birds removed the significance (but not direction) of the relationship. Distance of nests of known-age birds from the colony centre was negatively correlated with adult age ( $r = -0.61$ ,  $P = 0.001$ ,  $n = 32$ ) and nest construction, considered in categorised groups (Fig. 1), also suggested that completion was related to age. Thus, by late July, proportionally fewer nests, of those to be formed during the study, were present in the peripheral group compared with more central groups (Table 1): such differences were significant ( $\chi^2 = 11.04$ ,  $d.f. = 3$ ,  $P < 0.02$ ). Numbers of adults (banded or not) followed a similar pattern, with proportionately fewer birds than eventual nests being found early in the season in the outer nesting area ( $\chi^2 = 33.61$ ,  $d.f. = 3$ ,  $P < 0.0005$ ). Occasionally, younger breeding birds attempted to occupy central nest sites when these were unattended.

A severe storm (westerly winds  $> 60$  km/h) on 6 November 1994 coincided with the highest annual tides, raising local water levels and severely affecting parts of the study site. Seventy-one of 132 (54%) nests and contents, and three of four on rocks, were destroyed, most being washed away; losses in central nests were particularly extensive. Chicks died following displacement from destroyed nests, presumably



**Figure 2** Numbers of Australasian Gannets (■) and nests (◆) present at Pope's Eye, Port Phillip Bay, July–October 1994. (Birds nesting on adjacent rocks are excluded).

from exposure if not lack of food. Damage exceeded that recorded in more typical seasons (Norman & Menkhurst 1995), but re-laying began within a month in rebuilt nests.

### Eggs

Only one of 132 nests on the main structures never held an egg, and no clutch had two eggs. Some nests begun on rocks were inadequate and disappeared: these probably never contained eggs but, if laid, they would have rolled out without record. In this study, 142 nests were started, 140 first eggs were laid, 69 pairs re-laid and four pairs produced a third egg (second re-layings). Re-nesting and re-laying by marked individuals was always at previously used sites. Egg laying began between 26 August and 2 September (median 5 October 1994 for all eggs laid) and new eggs appeared for 16 weeks: this extended, and bimodal, laying was influenced by re-layings, particularly following the 6 November storm (Fig. 3). Mean laying dates for first eggs were earlier in the more central nests than those in outer groups (i.e. in group 4, 16 September  $\pm$  2.6 *s.e.* days,  $n = 27$ ; group 3, 17 September  $\pm$  2.2,  $n = 24$ ; group 2, 22 September  $\pm$  2.1,  $n = 46$ ; group 1, 11 October  $\pm$  3.6,  $n = 43$ ). The inter-group differences were significant (GLM;  $F = 17.84$ , *d.f.* = 3,  $P = 0.0001$ ) with group 1 showing significant differences with all other groups (Tukey studentised range test,  $P < 0.05$ ).

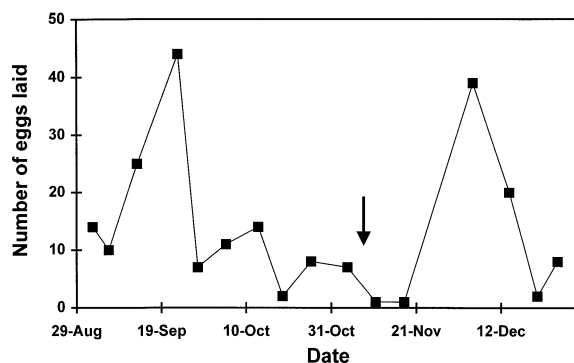
The mean mass of recently laid eggs was 99.5 g (*s.e.* = 0.69, range 82–118,  $n = 125$ ), and the volume index for all eggs was negatively correlated with date (Fig. 4) for those laid before 6 November 1994 ( $r = -0.28$ ,  $P < 0.001$ ,  $n = 142$ ). For 22 known-aged birds

(4–17 years old), there was no correlation between egg size and age, nor was there an indication (GLM) of differences between groups.

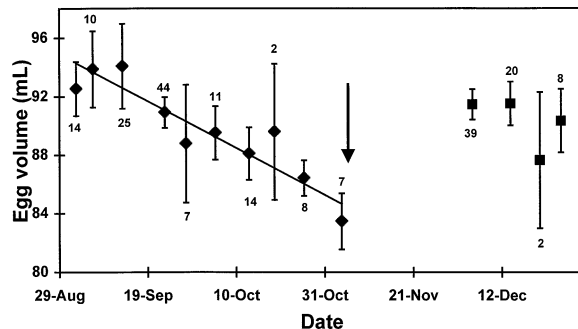
Volumes of re-laid eggs were highly correlated with those of corresponding first eggs ( $r = 0.70$ ,  $P < 0.001$ ,  $n = 69$ ), as were their shape indices ( $r = 0.63$ ,  $P < 0.001$ ). First eggs were, on average, smaller and lighter than re-laid eggs (Table 2) but differences were not significant (*t*-tests).

### Breeding attempts and breeding success

Of 140 first eggs, 88 (63%) hatched, 50 (36%) were lost and two, incubated for 120 and 164+ days (longer than previously recorded, Wingham 1984a), did not hatch.



**Figure 3** Numbers of eggs laid by Australasian Gannets between visits at Pope's Eye, Port Phillip Bay, 1994–95. The arrow indicates the time of the storm on 6 November 1994.



**Figure 4** Mean volume ( $\pm$  *s.e.*) of newly laid eggs of Australasian Gannets at Pope's Eye, Port Phillip Bay, in relation to date, before ( $\blacklozenge$ ) and after ( $\blacksquare$ ) the storm on 6 November 1994 (indicated by the arrow). The straight line indicates the significant negative correlation before the storm. Sample sizes indicated.

**Table 1** Occupied nests (% of those formed during the study) and numbers of adult Australasian Gannets present at Pope's Eye, Port Phillip Bay, Victoria, in each 'age' grouping. Excluded are nests and adults present at sites on adjacent rocks. (Group details as per Fig. 1.)

Parameter	Group			
	1	2	3	4
Per cent of nest total present by 26 July 1994	48.6	57.8	70.4	88.0
Per cent of nests occupied in August–September	60.0	100.0	100.0	88.0
Number of adults present	21	45	27	22
Number of vacant sites	14	0	0	3
Nest total	(35)	(45)	(27)	(25)

**Table 2** Mensural characteristics (width and length in mm, mass in g) of eggs of Australasian Gannets, Pope's Eye, Victoria, 1994–95. Details for first, second and third eggs are given.

Egg number	length ( $\pm$ s.e.)	Mean		mass ( $\pm$ s.e.)	n
		width ( $\pm$ s.e.)	n		
First eggs	78.51 (0.25)	47.96 (0.14)	140	98.3 (1.10)	57
Re-laid eggs	78.53 (0.37)	48.22 (0.15)	69	100.3 (0.87)	64
Second re-laid eggs	79.28 (1.75)	49.92 (0.94)	4	105.0 (4.65)	4
All eggs	78.53 (0.20)	48.06 (0.11)	213	99.5 (0.69)	125

Fifty-seven of 69 (83%) re-laid eggs hatched as did three of the four third eggs. For all 213 eggs laid, 70% hatched. Some 82% of nests with first eggs hatched a chick (115) but of these no more than 103 fledged (74% of eggs laid) and for all eggs laid (213) fledging success was 48%. Of 148 chicks hatched, 103 (70%) eventually fledged.

Although the proportions of hatched eggs resulting in fledged chicks showed some differences between groups (group 1, 41%; 2, 52%; 3, 65%; 4, 45%), they were not significant ( $\chi^2$ ), and nor were percentages of chicks fledged from occupied nests (group 1, 70%; 2, 82%; 3, 74%; 4, 88%). Group 1 adults lost more eggs than other groups ( $\chi^2 = 58$ , *d.f.* = 3,  $P < 0.005$ ), and there was a significant difference between groups in the proportion involved in re-laying ( $\chi^2 = 21.6$ , *d.f.* = 3,  $P < 0.005$ ). Replacement was lower than expected in group 1 nests (45%) but higher in group 4 (92%).

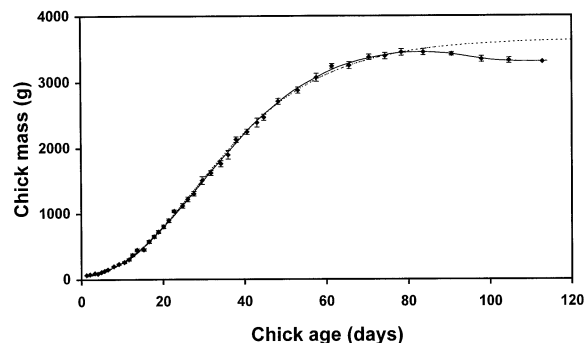
Most (84%) pairs that lost eggs or chicks in November re-laid (see below), compared with 38% following losses at other times, but 71% of all losses were replaced. There was no apparent relationship (*t*-test) between re-laying interval and stage of loss (egg, or chick), nor was there a difference ( $\chi^2$ ) in the proportions re-laid after loss of an egg, or a young ( $\leq 8$  days old) or older ( $> 8$  days) chick. First clutches, if lost, were replaced in 73% of cases, significantly more than the 33% second layings replaced ( $\chi^2 = 7.76$ , *d.f.* = 1,  $P < 0.01$ ). Three pairs that lost chicks before or after the storm did not re-lay.

### Chick growth

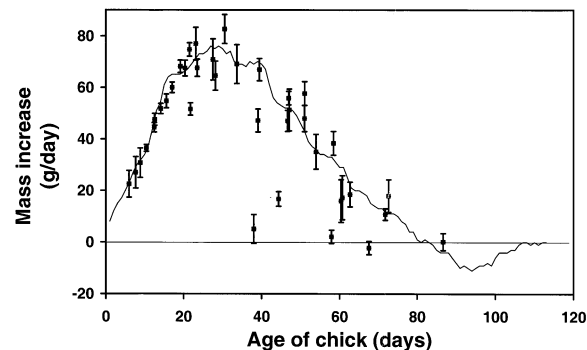
A Gompertz curve (Fig. 5) was fitted to the masses of chicks at various ages (following Ricklefs 1967), where

$k = 0.056$ , age at inflection point = 27.4 days and asymptote = 3650 g. Where ages were appropriate (3–55 days), the curve explained 97% of the variation ( $P < 0.001$ ,  $n = 529$ ). However, since chicks lost mass prior to fledging, a curve fitted by eye was more useful, allowing examination of relative changes in mass (Fig. 6). Mass increase was greatest when chicks were 15–45 days old, reaching a maximum of *c.* 80 g/day in chicks of about 30 days old.

Mean relative mass varied markedly between visits to the colony (Fig. 7), being considerably lower immediately following the November storm, and relative changes were weakly but significantly correlated with



**Figure 5** Growth of Australasian Gannet chicks (mass) from hatching to fledging; Pope's Eye, Port Phillip Bay, Victoria, 1994–1995. Indicated are mean values ( $\pm$  s.e.,  $n = 38$ ), a Gompertz curve (dashed line; following Ricklefs 1967) and a curve fitted by eye (solid line).

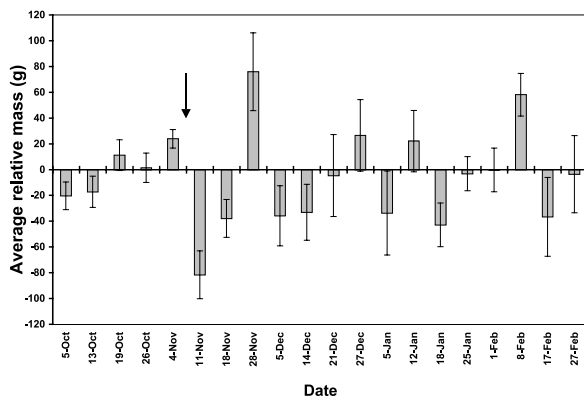


**Figure 6** Rate of growth of Australasian Gannet chicks in relation to age, Pope's Eye, Port Phillip Bay, 1994–95. The fitted curve is derived from the growth curve (Fig. 5), and data points are averages of  $> 20$  values  $\pm$  s.e.

the mean wind speed since the previous visit ( $r = 0.10$ ,  $P = 0.009$ ,  $n = 678$ ). The trivial  $r^2$  value (1%) indicated high individual variability (see also Wingham 1984b). Chicks from re-laid eggs had higher mean relative masses than first clutch chicks (paired  $t$ -test,  $t = -2.829$ ,  $d.f. = 27$ ,  $P = 0.009$ ,  $n = 28$ ), and their relative mass remained higher ( $141 \pm 70$  g above average,  $n = 14$ ) at last weighing (21 March 1995).

The maximum chick mass recorded was 3870 g (2 chicks, 95 and 98 days old) and the mean maximum, estimated from the fitted curve and reached at 80 days, was 3450 g (c. 130% of the adult mass given in Marchant & Higgins 1990). For chicks weighed beyond 80 days, the mean maximum mass was  $3521 \pm 58$  g ( $n = 37$ ) reached at  $86 \pm 4$  days (56–108,  $n = 37$ ). Increases were minimal near fledging, and some chicks declined in mass at that time.

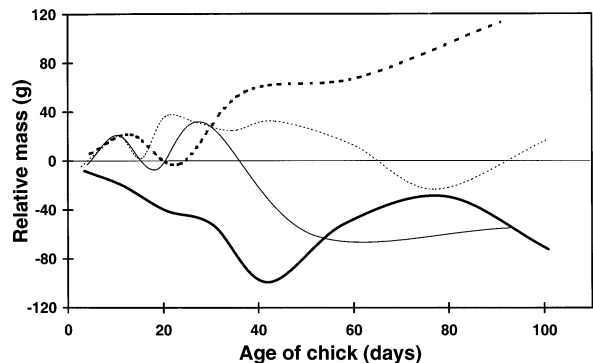
Relative chick mass at first measurement was significantly correlated with egg volume for all groups combined ( $r = 0.489$ ,  $P = 0.003$ ,  $n = 146$ ) but not with date of hatching for groups 1, 2 and 4. Group 1 chicks were typically 3.5 g lighter at first weighing, and group 3 chicks 4.4 g heavier, while groups 2 and 4 were within 0.5 g of average values. Subsequent growth patterns in the 40 days post hatching showed considerable differences between groups (Fig. 8), with the lighter, group 1 chicks falling further below the average. Although some mass was subsequently regained, these chicks had the lowest relative masses. Group 3 chicks were consistently above average throughout their growth, but group 4 chicks fell below it after about 40



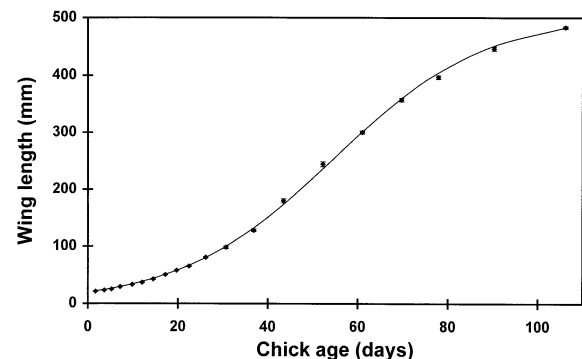
**Figure 7** Relative chick mass (differences from average growth curve) in Australasian Gannets in relation to date, Pope's Eye, Port Phillip Bay, 1994–95. The arrow indicates the storm on 6 November 1994.

days and remained so. Techniques for comparison of such growth patterns are unavailable (Bradley et al. 1995) but group 1 chicks had lower mean relative mass and growth rates than group 2 chicks (two-tailed  $t$ -test,  $t = -0.326$  to  $-0.372$ ,  $P < 0.05$ ). For up to about 100 days post hatching, relative chick mass in relation to age was almost always positive (and increasing) for group 3, usually positive but variable in group 2, mostly negative and declining in group 4 and always variable and negative in group 1 (which also showed a most dramatic decline in the first 40 days after hatching).

Wing length growth was examined using a logistic curve (Ricklefs 1967), in which  $k = 0.0589$ , age at



**Figure 8** Relative chick masses (differences from average growth curve) for Australasian Gannet chicks in the four age/site groups, in relation to age of chick; Pope's Eye, Port Phillip Bay, 1994–95. (Group details in Fig. 1.) Group 1-heavy solid line; Group 2-light dash; Group 3-heavy dash; Group 4-light solid.



**Figure 9** Wing growth (mean length,  $\pm$  s.e.;  $n = 38$ ) in chicks of Australasian Gannets, Pope's Eye, 1994–95. The logistic curve was fitted using the method of Ricklefs (1967).

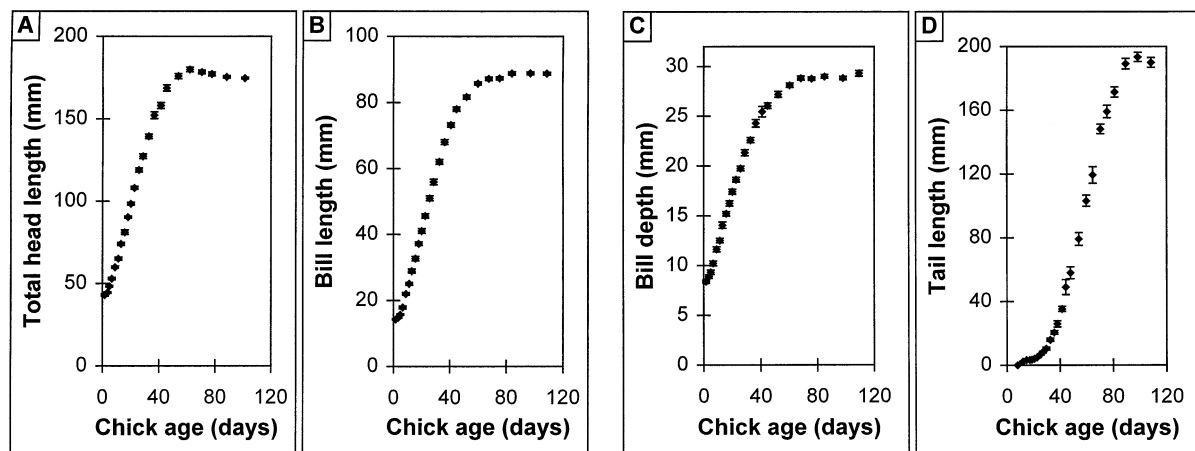
inflection point = 54.5 days, and asymptote 506 mm (Fig. 9). Relative wing growth (calculated as for relative mass) varied with date; it was significantly correlated with relative mass ( $r = 0.447$ ,  $P < 0.001$ ,  $n = 121$ ), and wings reached a mean maximum length of 465 mm (about that of adults, Marchant & Higgins (1990) gave means of 463–471 mm for small samples of males and females) when chicks were 90–106 days old. Changes in other measures (Fig. 10) show that growth levelled out well before fledging.

## Discussion

Reproductive parameters obtained in this study resemble those recorded previously at Pope's Eye (Norman & Menkhurst 1995), reflecting a constancy in pattern during five breeding periods. There are, however, some differences when compared with Australasian Gannets, or related species, breeding elsewhere. Thus, nest densities at Pope's Eye were similar to those reported earlier (1.6 nests  $m^{-2}$ ), but lower than recorded at other colonies (1.9–2.6) or in those of Northern Gannets *Sula bassana* (2.1; see Wingham 1984a for details). The reduced density at Pope's Eye may result from the artificial topography affecting nesting opportunity, and/or varying methods of calculation, but it is variable in gannets generally (Nelson 1978b). Similarly, start of laying and mean laying dates were similar to previous records, but slightly later than found in New Zealand, and eggs at Pope's Eye were larger than those at New Zealand colonies (Wingham 1984a; Norman & Men-

horst 1995; this study). Re-laying after the November storm resulted in extended laying (longer than previously recorded at Pope's Eye, or found in New Zealand), a higher rate of re-laying (71% compared with c. 50% in New Zealand, Wingham 1984a), and fewer chicks fledged per egg laid (48 cf. 57%, Norman & Menkhurst 1995).

At Pope's Eye, older birds tended to nest more centrally (Fig. 1). This occurs in other seabird colonies (Coulson 1968; Ainley et al. 1983) but Nelson (1978b) considered that a gannet colony should be of uniform age distribution unless expanding. Since nest site fidelity is high in gannets (Nelson 1978a, b; Klages 1994), the distribution may reflect original colonisation (c. 1985, i.e. well within the lifespan of some birds breeding in 1994), even at an artificial and irregular site such as Pope's Eye. Such fidelity could mitigate against a completely older, central age cohort since younger adults may replace dead or non-reproductive older pairs that once nested there. Although peripheral sites may be of lower quality than more central sites (e.g. Ainley et al. 1983), this is not always so (e.g. California Gulls *Larus californicus*, Pugesek & Diem 1983) and in the present study, central nests were also extensively affected in a severe storm. Further, site quality cannot in itself affect variables such as laying date, egg size or chick growth where age or age-related factors must be involved. Since older adults have less future reproductive potential than younger ones, current efforts are of more importance. Increased reproductive efforts may occur in such adults to offset lower mean survival



**Figure 10** Growth of bill and head (total head length, A;  $n = 35$ ), bill (bill length, B, and bill depth, C; both  $n = 35$ ), and tail (tail length, D;  $n = 25$ ) in Australasian Gannet chicks, Pope's Eye, Port Phillip Bay, 1994–95. Points are means  $\pm$  s.e.



(Curio 1983, but see Charlesworth 1980) resulting in greater 'effort' by birds whose physical condition and survival is declining (Clutton-Brock 1988): this effort would be enhanced by, or just reflect, any improvements related to age and experience. Parental age may affect aspects of breeding events, including reproductive success, in various ways. Thus, more experienced birds have more stable, longer formed pair bonds, perhaps have nest sites with enhanced quality and so may breed earlier, irrespective of seasonal conditions: they may also produce more young and be more efficient in dealing with predators (e.g. Nol & Smith 1987; Bradley et al. 1990; Shaw 1995). Similarly, foraging efficiency may increase with age (e.g. Brown Pelicans, Orians 1969; Blue Herons *Ardea herodias*, Quinney & Smith 1980). All Gannet pairs presumably have similar foraging opportunities while breeding, so increased efficiency with age could allow earlier egg formation and laying in older females.

Energy invested in reproduction varies as the breeding period progresses, reflecting changes in food availability, feeding rates or competition costs (Stutchbury & Robertson 1988), and also varies between individuals, much of which may be age-related. The relationship between decreasing egg size and laying date in Gannets, as in Southern Fulmars *Fulmarus glacialis* (Weimerskirch 1990) and Silver Gulls *Larus novaehollandiae* (Mills 1979), probably reflects changes in ability to invest. Weimerskirch (1990) showed that it was inexperienced female Southern Fulmars that produced the smaller later eggs. This pattern was evident within groups at Pope's Eye, presumably since younger Gannets arrived and laid later than older birds. Egg size was correlated with chick mass at first weighing, and chick mass at hatching influences early survival in other seabirds (Parsons 1970; Ankney 1980; Wingham 1984b). Early chicks from younger Gannets usually weighed less than average (and those from older Gannets generally more), which suggests they had reduced chances of survival. At Pope's Eye, the percentage of chicks fledged from eggs laid (in first and re-laid clutches) did not differ between groups, although there was some increased success in more central nests.

Relationships between chick growth and parental age have been little examined in seabirds (Ricklefs 1967), but studies relating fledging mass and or feeding efficiency, or comparing growth curves between species, are more common (Ainley et al. 1983; Gales 1984). Nevertheless, Lequette & Weimerskirch (1990) found early (but not later) chick growth was slower in

inexperienced pairs of Wandering Albatross *Diomedea exulans*, suggesting a lesser feeding efficiency early in the guard stage; they considered that efficiency was not enhanced with later attempts. In this study, chicks of peripheral, group 1 (younger) adults had a lower mass and mass increased at a lower rate than average for the first 40 days post-hatching, suggesting that the parents were less efficient providers than older (more experienced) birds in this period. Certainly chicks of more central (older) adults showed variation in relative mass in relation to age but the index usually favoured inner groups, perhaps indicative of minor qualitative differences. If chick mass at c. 100 days approximates fledging mass (110 days for Australasian Gannets, Wingham 1984b), then chicks of group 1 adults fledged lighter than others. Of note was the relatively higher mass of group 3 chicks compared with those of group 4 (presumed oldest) adults (Fig. 8), reflecting comments by Wooller et al. (1990) who found that adults with most experience had a lower success than those of intermediate age. Fledging mass influences post-fledging survival in the Cape Gannet *Morus capensis* (Jarvis 1974), so increasing chick mass around fledging may be one way of increasing LRS.

Some sulids produce more than one egg per clutch (Nelson 1978b), presumably another way of enhancing LRS. However, at least in the Brown *Sula leucogaster* and Masked *S. dactylatra* Boobies, only one chick survives (Simmonds 1967), and clutch size in gannets appears to be restricted to a single egg, even though two chicks can be raised (Navarro 1991). Here the relative improvement in LRS is important, and is perhaps maximised in gannets by marginal increase in (age-related) efficiency needed to increase chick mass, and hence reproductive success, rather than the more substantial effort needed to produce larger clutches of smaller chicks. Success is also enhanced by pairing and laying earlier, which is more likely in older birds with a longer-established partnership.

Younger breeding adults, which have a greater reproductive potential than older birds, may be less committed to (or prepared for) immediate reproduction. If this occurs in a long-lived species such as the Gannet, it should be reflected in lower hatching and fledging success in younger cohorts. In California Gulls, where a reduced commitment (effort) by younger birds occurs, its importance may influence interpretation of reproductive ability (Pugesek 1981; Curio 1983). The severe storm at Pope's Eye, which disproportionately affected group 4 (oldest) adults reduced the opportunity to

examine other aspects of reproductive effort. Nevertheless, that group 1 birds replaced fewer lost eggs, and group 4 birds more, than average suggests a reduced reproductive effort by younger birds. Again, since Gannets can re-lay after egg or chick loss, earlier laying and enhanced chick growth may improve LRS more than increasing clutch size.

Food availability may influence reproductive state in some gannet species (Adams & Walter 1991) and starvation of chicks may be high during rough weather (Waghorn 1982, Navarro 1991), either directly from lack of food returns or from increased thermoregulatory demands. To an extent weather conditions (e.g. wind speed) influenced chick growth in this study, perhaps reflecting variation in foraging efficiency where prey distribution, visibility and availability may be affected (see also Dunn 1973, 1975; Birkhead 1976). However, chicks at Pope's Eye were heavier than reported elsewhere, suggesting ready availability of food for this population (see also Nelson 1978a; Navarro 1991). Food availability, for Australasian Gannets (in New Zealand, Wingham 1984b) or Cape Gannets (Jarvis 1974), may be lower at other times or sites. Chick growth was more rapid at Pope's Eye, and mass at similar age higher, than Wingham (1984b) found, again suggesting sufficient food availability, although fledging occurred at similar ages.

Seasonal (and climatic) factors in Port Phillip Bay differ from those at colonies in New Zealand where breeding is earlier and more synchronised. At Pope's Eye, the age of Gannets influenced arrival at the colony, nest location, laying date, chick mass and fledging success. The trend found here (where 'age' grouping was extrapolated from the distribution of known-age birds) was for generally improved chick growth and breeding success with increased age, a plateau for older birds and, in some parameters, a decline in the oldest age group. While changes in foraging efficiency may be sufficient explanation, variation in individual effort may also be important, and current data do not permit examination of individual differences in adult quality (e.g. Newton 1989). The single-egg clutch of Australasian Gannets appears to be explicable in terms of current evolutionary theory as Gannets can increase annual reproductive success with age (in a stable pair) by adjusting the time of laying and by the production of heavier chicks earlier in the breeding period. Post-fledging survival may be studied further to determine whether LRS is in fact enhanced by adult age. However, such a study is not possible at Pope's Eye since

there is no longer an extensive area available for young produced to return to breed.

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