REPRODUCTIVE SUCCESS AND CHICK GROWTH OF PACIFIC GULLS LARUS PACIFICUS IN THE FURNEAUX GROUP, AUSTRALIA

LUCY WIDDUP

Department of Environmental Management and Ecology, La Trobe University, Wodonga, Victoria 3690, Australia (lucy@widdup.net) Present Address: 8 Indigo Close, West Wodonga, Victoria, 3690

Submitted 20 January 2013, accepted 27 August 2013

SUMMARY

WIDDUP, L. 2013. Reproductive success and chick growth of Pacific Gulls *Larus pacificus* in the Furneaux Group, Australia. *Marine Ornithology* 41: 187–194.

The Pacific Gull *Larus pacificus* is a large larid endemic to Australia, widespread in the southern half of the continent. Little is known about its breeding biology. I present data from 131 nests across nine islands in the Furneaux Group, Tasmania. Pacific Gulls demonstrated a protracted laying period between 16 October 2003 and 2 January 2004, producing on average 2.11 ± 0.64 eggs per clutch. Egg size and mass decreased through the laying sequence. Eggs from three-egg clutches were larger and had greater mass than eggs from smaller clutches. Overall, 45% of eggs hatched, with wide disparities in hatching rates among islands. Solitary pairs were most successful, hatching 100% of their eggs. Estimation of growth over the first 60 days of chicks' life displayed an S-shaped curve, typical of logistic growth, but none reached the parental asymptotes for any of the body measurements. Overall reproductive success was 26%. As with hatching, pairs nesting solitarily on islets had the highest fledgling success. Amongst islands with more than one nest, Mid Woody Island had the highest fledgling success, with 52% of all nests initiated having a chick survive. Pacific Gulls are threatened by increased urbanisation, anthropogenic disturbance and possibly intra-specific competition from Kelp Gulls *L. dominicanus*. These data are the first to be published from the Furneaux Group and will assist in the future management of the species.

Key words: Australia, Furneaux Group, Larus pacificus, Pacific Gull, species threats, Tasmania

INTRODUCTION

There are three resident gull (Charadriiformes: Laridae) species in Australia: the Silver Gull Chroicocephalus novaehollandiae, Pacific Gull L. pacificus and the recently arrived Kelp Gull L. dominicanus (McGill 1943, Higgins & Davies 1996). The Pacific Gull is Australia's largest gull and is endemic to southern Australia, restricted to the coast from offshore islands in Victoria, Bass Strait, Tasmania, west to Shark Bay in Western Australia (Serventy et al. 1971, Burbidge and Fuller 1989, Fuller et al. 1994, Burbidge and Fuller 2004, Surman and Nicholson 2009). The greatest abundance occurs in the Furneaux Group, Tasmania (Brothers et al. 1996). Two subspecies have been recognised, the nominated eastern subspecies L. p. pacificus and the western subspecies L. p. georgii. Recent estimates indicate the population to be approximately 11000 individuals. The population is suspected to be stable in the absence of evidence of any significant declines or substantial threats (Birdlife International 2013), and it is listed as Least Concern under the IUCN Red List (Birdlife International 2013). On the east coast of Australia there has been speculation that their breeding range has contracted (Serventy et al. 1971), possibly as a result of disturbance and urbanisation of their preferred nesting and foraging habitat. Apart from minor studies of population trends in Hobart, Tasmania (Coulson & Coulson 1998), and of diet (Coulson & Coulson 1993; Lindsay & Meathrel 2008), little ornithological work has been undertaken on Pacific Gulls. Much of the breeding biology of this species remains unquantified and speculative. The aims of this study were to collect baseline data on the reproductive success and chick growth of Pacific Gulls breeding in the Furneaux Group, including timing of breeding, egg and clutch size, hatching success, fledging success and chick growth rates. These data are the first to be published on this species from the Furneaux Group.

METHODS

Study area

Research was carried out on nine islands within Franklin Sound, Furneaux Group, Tasmania (148°E, 40°S) (Fig. 1): Briggs Islet, Cook Islet, Fisher Reef, Spences Reef, Little Dog Reef, Great Dog Island, Ram Island, Tin Kettle Island and Mid Woody Island. Islands ranged in size from 0.1 ha to 353 ha. The larger islands support remnant stands of Tasmanian blue gum *Eucalyptus globulus globulus* forest, swamp paperbark *Melaleuca ericifolia* and coastal tea-tree *Leptospermum laevigatum* dominating the vegetation, whereas the smaller islands are low, open and dominated by coastal tussock grass *Poa poiformis* and other coastal species of small scrub. The islands monitored during this project are typical for this region. Attributes of each island including geology, vegetation and other breeding seabirds are detailed in Harris *et al.* (2001) and Brothers *et al.* (2001).

Nest monitoring

On the first visit to the islands, all Pacific Gull nests that had been marked during the 2000–2001 (Holloway 2001) and 2002–2003 (unpublished data) seasons were assessed for activity. Searches were made of the entire islands to locate new nests before egglaying. Visits to islands were made three days apart or more, for a maximum of two hours, as prescribed by university animal ethics permits. This interval was used to standardise the duration of researcher disturbance that each island received. However, visits to the island varied from once every three days to once per month owing to adverse weather conditions. A nest was determined as "active" when there was an egg present. The sequence of egg-laying within a clutch (a-egg, b-egg and c-egg, being the first, second and third, respectively) was recorded by marking the blunt end of the egg with non-toxic brown nail polish. As islands were not visited daily, the order of egg-laying in many cases was unknown. In this instance, the laying sequence was assigned by comparing the size and shape of the pigmentation and the pattern on the shells following Wooller & Dunlop (1979) and Nawrocki (1989). The maximum length and width of each egg were measured to within 0.02 mm using Vernier callipers. Egg volume was calculated using the formula $v = klb^2$, where k was the constant 0.476 (Parsons 1976), 1 is the length and b is the breadth of the egg. Egg mass was measured to the nearest 1 g using 200 g Pesola spring scale. On each visit the status of the eggs was recorded. The fate of all eggs was categorised as failed, hatched or unknown. Failed included outcomes such as addled, predated (crushed or punctured shell), dead in star (shell cracked but hatching incomplete), or dead in pip (shell penetrated but chick remained trapped). Unknown included all outcomes where there was no firm evidence of hatching. Once eggs began to star or pip, the hatch date could be predicted to be in 5 d or 2 d, respectively. If the exact day of hatching was unknown, the age of the chick was estimated from the star and pip dates in addition to using chick growth data collected previously (Holloway 2001).

Hatching success was considered when at least one egg from the clutch hatched. Reproductive success was defined as the number of nests that had hatchlings survive through to fledgling divided by the total number of nests initiated.

Chick growth

Approximate hatching dates were determined by estimating the age of the chick on the first visit after hatching (i.e. its size as compared to growth data presented in Holloway [2001]), and back-calculating to the day of hatching. Morphometric measurements were recorded each time a chick was handled to assess growth. Total head length,



Fig. 1. Location of Flinders Island, Furneaux Group, Australia. Research was carried out on nine islands within Franklin Sound, the body of water between the two largest islands in the Furneaux Group, Flinders Island and Cape Barren Island.

bill gape, bill depth at the gonys and outer tarsus were measured with Vernier callipers to within 0.02 mm after Baldwin *et al.* (1931). The wing (hand) length, plus the 10th primary feather once it erupted, were also measured using a wing ruler to the nearest 1 mm. Chicks up to 1 kg were weighed using Pesola 1 kg scales to the nearest 5 g. Chicks over 1 kg were weighed using Pesola 5 kg scales to the nearest 25 g. All chicks that weighed >150 g were banded with individually numbered Australian Bird and Bat Banding Scheme (ABBBS) stainless steel bands. Once chicks were >300 g, they were colour-banded using Darvic colour bands following the ABBBS schema 13, in which a colour band is placed above the metal band on the right leg and two colour bands are placed on the left leg, allowing individuals to be identified at a distance later in the breeding season.

Statistical analysis

All statistical analyses were carried out using SPSS Version 12.0 for Windows (SPSS Inc. 2003), following Sokal & Rohlf (1995). All values are presented as mean \pm standard error, and the level of significance is set at 0.05, unless otherwise stated.

RESULTS

Breeding period

Over the 2003–2004 austral summer, I monitored 131 nests. In total, 277 eggs were laid, the first on 16 October, as backcalculated from hatching day (i.e. minus the 27 d incubation period reported for Pacific Gulls [Holloway 2001]). For the nine islands studied, eggs were present on the first visit to four islands: Ram Island, Briggs Islet, Tin Kettle Island and Cook Islet. The last egg laid was found on Briggs Islet on 2 January, suggesting an egglaying period of 78 d. The peak egg-laying period was consistent for all islands except Briggs Islet, on which the egg-laying season extended over 69 d. On Great Dog Island and Spences Reef, clutch initiation occurred in mid-November, slightly later than on the other islands. However, at this date, approximately 50% of eggs had been laid on Briggs Islet.

TABLE 1 Clutch size of complete clutches for Pacific Gulls breeding in Franklin Sound, Tasmania, 2003–2004, by island

Island or islet	Number of nests	Mean ± SE
Mid Woody	31	2.03 ± 0.09
Ram	18	2.39 ± 0.14
Briggs	60	2.00 ± 0.09
Tin Kettle	13	2.08 ± 0.21
Cook	4	2.50 ± 0.29
Great Dog	2	2.50 ± 0.50
Spences Reef	1	2.00
Little Dog Reef	1	3.00
Fisher Reef	1	3.00
Total	131	2.11 ± 0.06

Clutch and egg size

Clutch size ranged from one to three eggs and was defined as the maximum number of eggs present in a nest over the time of monitoring. The clutch size for Pacific Gulls nesting across all nine sites was 2.11 ± 0.64 eggs (Table 1). A one-way ANOVA with island as the factor revealed that there was no difference between the clutch sizes of Pacific Gulls nesting on different islands (F_{8,122} = 1.55, P > 0.05).

The mean size of eggs from each island was compared (Table 2). With clutch sizes combined, neither egg length (range 67.06–83.20 mm; $F_{8,268} = 1.79$, P > 0.05) nor egg mass differed among islands (range 80–132 g; $F_{8,268} = 1.56$, P > 0.05). Egg width and volume differed (range 43.30–54.34 mm; range 61.92–106.18 cm³; $F_{8,268} = 2.50$, 2.88, respectively, both P < 0.01). However, SNK post hoc testing failed to identify the islands that had eggs of different size. As a consequence, egg data were pooled across islands for subsequent analysis.

Size of eggs within the laying sequence (a-, b- and c-eggs) was compared using one-way ANOVA followed, where necessary, by Scheffé's post hoc testing, using the data combined across islands (Table 3). Egg length did not differ within the laying sequence ($F_{2,274} = 0.92$, P = 0.40). However, c-eggs were narrower and had a lower volume than a-eggs or b-eggs within a clutch ($F_{2,274} = 3.48$, 3.98, respectively, both P < 0.03). On average, the c-egg was also less massive than either the a- or b-egg within its own clutch ($F_{2,274} = 6.10$, P < 0.03).

The size and mass of eggs occupying the same position in the laying sequence were compared between the clutch sizes. Length, width,

volume and mass were compared for a-eggs between the three clutch sizes using a one-way ANOVA followed, where necessary, by Scheffé's post hoc testing, and using the data combined across all islands (Table 4). Length did not differ between the a-eggs from 1-, 2- or 3-egg clutches ($F_{2,128} = 1.79$, P > 0.05). The width and volume of the a-egg from 3-egg clutches were greater than those from 1- or 2-egg clutches ($F_{2,128} = 11.21$, 8.13, respectively, both P < 0.01). A-eggs from 1- and 2-egg clutches had the same length, width, volume and mass (all P > 0.05). However, the a-egg from 3-egg clutches was heavier than a-eggs from either 1- or 2-egg clutches $(F_{2,128} = 6.74, P < 0.00)$. As only 2- and 3-egg clutches had a second egg, the size and mass of b-eggs were compared using Levene's test for equality of variance, followed by a 2-tailed Student's t-test. The variance of the length, volume and mass of b-eggs were found to be equal, whereas, for width, the assumption of equal variance was not upheld. The length of b-eggs was the same between clutch sizes (t_{109} = -1.45, P = 0.15). However, the width, volume and mass of b-eggs were larger for the second egg from 3-egg clutches than the second egg from 2-egg clutches ($t_{96.45} = -4.74$, $t_{109} = -4.00$, $t_{109} = -4.35$, respectively, all P < 0.01). Overall, egg size and mass were greatest for 3-egg clutches compared with smaller clutches, and smallest for last laid eggs within a clutch of any size.

Reproductive success

The fate of 44% of eggs that disappeared between visits was unknown, and hatching success (expressed as the percentage of eggs laid that hatched) was 45% with significant differences among islands ($\chi_{210} = 40.42$, P < 0.01). Overall, an average of 17% of eggs failed to hatch, with wide disparities between islands. The hatching success for gulls nesting solitarily on Great Dog Island, Fisher, Spences and Little Dog Reefs was 100%, but success was much

		Mean ± SE						
Island or islet	Ν	Egg length (mm)	Egg width (mm)	Egg volume (cm ³)	Egg mass (g)			
Briggs	120	74.34 ± 0.26	50.49 ± 0.14	90.32 ± 0.64	108.12 ± 0.71			
Mid Woody	64	73.27 ± 0.33	50.14 ± 0.25	87.89 ± 1.05	107.30 ± 1.16			
Ram	43	74.84 ± 0.38	51.15 ± 0.17	93.26 ± 0.81	110.98 ± 1.18			
Tin Kettle	27	74.77 ± 0.65	51.21 ± 0.25	93.43 ± 1.27	111.44 ± 1.67			
Cook	10	74.83 ± 1.13	50.51 ± 0.34	90.83 ± 1.36	109.90 ± 1.72			
Great Dog	5	75.12 ± 1.16	50.27 ± 0.86	90.34 ± 2.37	111.00 ± 1.90			
Spences Reef	2	74.25 ± 1.88	51.78 ± 0.94	94.74 ± 1.05	114.50 ± 0.50			
Little Dog Reef	3	71.50 ± 1.52	51.27 ± 0.20	89.46 ± 2.26	110.33 ± 3.18			
Fisher Reef	3	74.51 ± 0.28	51.93 ± 0.41	95.65 ± 1.84	115.67 ± 2.33			
Total	277	74.21 ± 0.17	50.61 ± 0.10	90.62 ± 0.43	109.00 ± 0.49			

 TABLE 2

 Egg size and mass for Pacific Gulls breeding in Franklin Sound, all clutch sizes combined

TABLE 3

Size and mass of a-, b- a	and c-eggs, pooled a	cross clutch sizes, for Pacific	c Gulls breeding in Franklin Sound
---------------------------	----------------------	---------------------------------	------------------------------------

Egg	n	Length (mm)	Width (mm)	Volume (cm ³)	Mass (g)
А	131	74.43 ± 0.26	50.80 ± 0.14	91.57 ± 0.65	110.50 ± 0.65
В	111	74.11 ± 0.27	50.58 ± 0.15	90.38 ± 0.66	108.37 ± 0.84
С	35	73.75 ± 0.46	50.01 ± 0.21	87.82 ± 0.89	105.43 ± 1.22

 TABLE 4

 Egg size and mass, separately by a- and b- eggs, in differentsized clutches laid by Pacific Gulls breeding in Franklin Sound

		Clutch size, mean ± SE					
	Egg	One, n = 20	Two, n = 76	Three, n = 35			
Length	а	74.97 ± 0.75	74.97 ± 0.75	75.01 ± 0.43			
(mm)	b	_	73.85 ± 0.34	74.68 ± 0.42			
Width	а	49.75 ± 0.38	49.75 ± 0.38	51.71 ± 0.19			
(mm)	b	_	50.19 ± 0.19	51.43 ± 0.18			
Volume	а	88.42 ± 1.58	90.56 ± 0.87	95.55 ± 1.01			
(cm ³)	b	—	88.69 ± 0.82	94.05 ± 0.83			
Mass	а	108.50 ± 1.62	109.29 ± 0.85	114.26 ± 1.08			
(g)	b	_	106.07 + 1.01	113.37 ± 1.14			

lower on Ram Island and Briggs Islet (approximately 25%). On average, nests on Mid Woody Island, Tin Kettle Island and Cook Islet hatched 50% of eggs laid. The fate of more than half (60%) of eggs from Briggs Islet could not be ascertained. For islands with more than four nests, there were differences between fates among islands ($\chi_{26} = 38.28$, P < 0.01). Pacific Gulls nesting on Mid Woody Island had the highest percentage of successful nests (80%). The lowest percentage of successful nests occurred on Briggs Islet, with only 30% of all nests producing at least one hatchling. Overall, the fate of individual eggs, and individual nests, differed among islands. Solitarily nesting Pacific Gulls had the lowest success (approximately 25% of eggs, or 50 % of nests).

The final number of fledglings was calculated for each island according to the actual number of chicks observed to survive to swimming and/or flight capability. From a total of 131 initiated nests, 71 (54.2%) nests had eggs that hatched. From this, 34 (48%) nests had hatchlings that survived through to fledgling (Table 5).

TABLE 5
Fledging success (number of nests that produced a hatchling that survived to fledging divided
by the total number of initiated nests) of Pacific Gulls breeding in Furneaux Group, Australia

Island or islet	Total nests (A)	Nests where eggs hatched (B)	% nests hatching at least 1 young (B/A)	Nests where chicks fledged (C)	% nests fledging at least 1 young (C/A)	% nests hatching young where at least 1 young fledged (C/B)	Total eggs laid (D)	Eggs hatched (E)	% hatching success (E/D)	Chicks fledged (F)	% fledging success (F/D)
Briggs	60	18	30.00	7	11.67	38.89	120	34	28.33	8	6.67
Mid Woody	31	25	80.65	16	51.61	64.00	64	49	76.56	22	34.38
Ram	18	11	61.11	3	16.67	27.27	43	11	25.58	3	6.98
Tin Kettle	13	10	76.92	5	38.46	50.00	27	16	59.26	5	18.52
Cook	4	2	50.00	1	25.00	50.00	10	4	40.00	2	20.00
Great Dog	2	2	100.00	0	0	0	5	5	100.00	0	0
Spences Reef	1	1	100.00	1	100.00	100.00	2	1	50.00	1	50.00
Little Dog Reef	1	1	100.00	0	0	0	3	3	100.00	0	0
Fisher Reef	1	1	100.00	1	100.00	100.00	3	2	66.67	1	33.33
Total	131	71	54.20	34	25.95	47.89	277	125	45.13	42	15.16

 TABLE 6

 Growth model analysis for morphometric data from measurements taken of Pacific Gull chicks

	Growth model							
Measurement	L (estimated asymptote)	b (slope of curve)	k (rate constant)	R ² (coefficient of determination)				
Head length (mm)	131.12	1.67	0.06	0.98				
Bill gape (mm)	83.00	1.93	0.06	0.95				
Bill depth (mm)	25.07	1.65	0.05	0.96				
Tarsus length (mm)	89.31	1.73	0.08	0.96				
Mass (g)	1158.67	13.42	0.12	0.96				
Wing length (+ 10th primary) (mm)	429.75	27.09	0.09	0.93				

Fledging reproductive success for Pacific Gulls nesting in Franklin Sound was 26%. Pairs nesting solitarily on the reefs and islets had the highest fledgling success. For islands with more than one nest, Mid Woody Island had the highest fledgling success, with 52% of



Fig. 2. The relationship between (A) head length, (B) bill length, (C) bill depth, (D) tarsus length, (E) body mass and (F) wing (+ 10th primary) length and age of Pacific Gull chicks (n = 130). Observations denoted by dots; predicted value denoted by lines.

all nests initiated having a chick survive to fledge ($\chi_{21} = 37.28$, P < 0.05). In summary, Pacific Gulls nesting on Mid Woody and Tin Kettle Islands had the greatest hatching and fledging success.

Chick growth

Newly hatched chicks were often found within 1 m of the nest site, and chicks moved up to 3 m at approximately 7 d of age. To find older chicks, searches were made up to 15 m from the nest. All searches were aborted when the chicks could not be found within 10 min. In these cases, the chick was recorded as missing, rather than dead or predated. As the breeding season progressed, the chicks moved to protective cover closer to the shoreline. With capture of the chicks becoming progressively more difficult, overall chick growth data were combined in order to establish the general growth pattern of pre-fledging Pacific Gull chicks in this study.

Growth curves were estimated using a non-linear regression growth model for all chick measurements, using the equation P(t) = L / (1 + L) $b \times exp^{-kt}$ where L = the estimated asymptote, b = the slope of the curve, k = rate constant, t = time (in this case, age of chicks in days) yielding P(t) = line of best fit (Bittinger 1996). This estimation of chick growth over the first 60 d of life displayed a S-shaped curve, typical of logistic growth, but none of the chicks reached the parental asymptotes for any of the body measurements. Because of a lack of published data available on asymptotic adult Pacific Gull body measurements, the asymptotes used for this analysis were computer-generated (Table 6). Head length, bill length, bill depth, tarsus length and mass (Fig. 2A-E) measurements had similar growth patterns, with rapid growth occurring from hatching through to day 40, when the rate of growth began to slow. Wing length (Fig. 2 F) had a much slower initial development up to day 15 before the 10th primary feather erupted, and the growth pattern was exponential.

DISCUSSION

For Pacific Gulls nesting in the Furneaux Group over the 2003–2004 austral summer, the degree of breeding synchrony among islands was variable. The egg-laying period was shortest, obviously, for solitary pairs and longest for the colony on Briggs Islet. Solitary breeders presumably experienced reduced levels of competition for resources compared with their colonial counterparts. This may explain why pairs of Pacific Gulls that nested solitarily began breeding slightly later than gulls nesting in groups. It may have been prudent for females in solitary pairs to delay laying until they were at their peak body condition, as egg-laying is a demanding process in semi-precocial birds (King 1973).

For Pacific Gulls nesting in groups, egg-laying synchrony among and within islands was high and ranged between four and six weeks. Gulls nesting in the southern hemisphere are generally synchronous (Yorio *et al.* 1995). However, Red-billed Gulls *C. scopulinus* in New Zealand have a protracted laying period extending over three months (Mills 1989), and Silver Gulls in Western Australia, have a breeding season that extends over eight months (Meathrel 1991). Similarly, Pacific Gulls breeding in the Furneaux Group have an egg-laying season that extended over a total of 78 d, or just less than three months.

Like other species of large gull (e.g. Herring Gull *L. argentatus* [Haycock & Threlfall 1975], Kelp Gull [Fordham 1964]), Pacific

Gulls laid clutches ranging from one to three eggs, with a modal clutch size of two. As is the case for many species of larid studied to date, there tended to be a decrease in egg size and mass through the laying sequence, reported to result from the depletion of nutrient reserves as subsequent eggs are laid (e.g. Meathrel & Ryder 1987, Meathrel *et al.* 1987, Bolton *et al.* 1993). As a result, the last laid egg in a clutch is smallest and has a lower hatching success within a clutch (Parsons 1970, 1975). Termed "the third-egg" or "third-chick disadvantage," last-laid eggs are viewed as insurance should an earlier-laid egg or chick be lost. This disadvantage has been studied extensively in a number of gulls, including Western Gulls *L. occidentalis* (Coulter 1980, Sydeman & Emslie 1992) and Herring Gulls (Kilpi *et al.* 1996).

There is a trade-off between clutch size and egg size in many gulls (see Reid [1987] for a review), so that eggs from smaller clutches are generally larger and more massive than those from larger clutches. However, Parsons (1970) noted a positive relationship between egg size, hatchling mass and fledgling survival in Herring Gulls. Herring Gulls that lay three-egg clutches were also found to be more likely to produce a hatchling than those laying one- or two-egg clutches (Paynter 1949, Brown 1967, Kadlec *et al.* 1969). This would suggest, therefore, that some hens are in better physiological condition and therefore better able to produce larger clutches of larger eggs without compromising their future survival (i.e. the cost of reproduction is a trade-off between current reproductive effort and future survival [Reid 1987]).

In this study, when the first-laid egg in a clutch was compared among clutch sizes, the a-egg from three-egg clutches was larger in width, volume and mass than those from smaller clutches. Likewise, the second-laid egg in a clutch was larger in width, volume and mass in three-egg clutches than the second-egg laid in two-egg clutches. This indicated that the energy (lipid and protein) investment for a hen laying three eggs was greater than hens laying fewer eggs (Meathrel & Ryder 1987, Meathrel et al. 1987, Bolton et al. 1992). Studies have shown that more experienced hens lay more, and larger, eggs. This may be due to a combination of breeding experience, body condition and foraging efficiency (Coulson et al. 1969, Mills 1979, Mills & Shaw 1980, Furness & Monaghan 1987, Harris & Wanless 1997). That some hens lay larger clutches, of larger eggs, has also been documented for the Glaucous-winged Gulls L. glaucescens (Reid 1988). As reported for Silver Gulls nesting in Western Australia (Lamont 2004), it would thus appear that hens laying clutches of three large eggs may be "super hens," as compared with those laying just one or two. The "super hens" may be able to reach a greater level of nutrient reserves (i.e. be in better physiological condition) required for egg formation and laying at an earlier date than those laying smaller clutches of smaller eggs.

Given the changeability of weather conditions in Bass Strait, a regular schedule of observations on the reproductive success of Pacific Gulls breeding in Franklin Sound was not possible, and the fate of 44% of eggs was unknown. As a consequence, this study may represent a potential underestimate of hatching success (of individual eggs, 40%), since eggs that had an unknown fate may have hatched successfully but were not recorded (i.e. because the chick was never found). Even with more frequent and regular nest checks, gull eggs and chicks are known to disappear between visits. For instance, Davis & Dunn (1976) found that 18% of Lesser Blackbacked Gull *L. fuscus* eggs disappeared between visits when nests were visited every other day. Similarly, Fordham (1964) reported

that 19% of Kelp Gull eggs in a New Zealand study disappeared over the incubation period. Fordham (1964) also reported that 50% of eggs that failed to hatch were addled, 21% were eaten by gulls or destroyed, 6% died while in star or pip, and a further 3% were lost through nest abandonment or destruction. The high rates of egg loss (i.e. fate recorded as unknown) and failure to hatch (i.e. addled, dead in star, dead in pip; 17% with a known failed fate) reported for Pacific Gulls in this study resulted in an overall hatching success of eggs of only 40%. This is below the 66% reported for Kelp Gulls by Fordham (1964) and the 65% reported by Davis & Dunn (1976) for Lesser Black-backed Gulls. Although this discrepancy seems large, it was most likely attributable to the *ad hoc* regime of visiting nests of Pacific Gulls enforced by inclement weather in Bass Strait.

In this study, the growth of Pacific Gull chicks followed the same growth pattern as reported for other larid species (e.g. Mineau et al. 1982, Reed et al. 1998, Sanchez-Guzmán & Muñoz del Viejo 1998, Nisbet et al. 1999, Risch & Rohwer 2000). Growth for head length, bill length and bill depth followed a linear pattern up to approximately 30 d of age. The chicks followed in this study did not reach the adult asymptotes for any body measurement, as is common in birds with delayed sexual maturity (Ricklefs 1968). Because Pacific Gulls are ground-nesting birds, chicks need to be able to move to protective cover early in their development (Lack 1968). In this study, the tarsus length of chicks at hatching was approximately 30% of an adult's tarsus length. The rapid increase in tarsus length over the first 30 d was thus indicative of the selection pressures on ground-nesting birds. Conversely, the development of wings was delayed until much later in the time taken to fledge. At hatching, the wing length of chicks was only 3% that of an adult. The rate of wing development was almost exponential over the chick-rearing period. Gulls have a relatively long chick-rearing period. Fisher & Lockley (1989) reported fledging ages from growth data for the Black-headed L. ridibundus, Common L. canus, Herring and Greater Black-backed L. marinus Gulls to be 40, 30, 42 and 50 d, respectively. The youngest a Pacific Gull chick in this study was observed to fledge (i.e. was capable of flight) was at 40 d of age. Most chicks tended to fledge around 50 d.

Although there was no difference in parental investment in egg production across islands (i.e. clutch size and egg size did not vary across islands), the success of nests varied greatly, from 100% fledging success for most pairs of Pacific Gulls nesting solitarily to only 12% for those nesting on the colony on Briggs Islet. Holloway (2001) reported that only 7% of nests on Briggs Islet produced a fledgling, so fledging success is variable between years, as it is for Red-billed Gulls (Mills 1989). Fledging success was greatest for those pairs nesting on Mid Woody Island (52%). The relatively greater success of gulls nesting on Mid Woody Island may have resulted from age-related factors; these gulls may have been older, more experienced or in better body condition (i.e. of higher physiological quality) than gulls nesting elsewhere, particularly Briggs Islet. In future studies, it would be worthwhile to determine the effects of parental quality on clutch size, egg size and the fate of eggs and nests by the use of brood enlargement and/or supplemental feeding studies, as has been done with a number of northern hemisphere species (e.g. Lesser Black-backed Gulls, Bolton et al. [1993]). Future studies might also consider concentrating on one or two larger colonies, rather than spreading fieldwork over multiple sites, in order to reduce the impacts of unpredictable weather conditions on fieldwork.

ACKNOWLEDGEMENTS

This study was carried out in accordance with La Trobe University Animal Ethics Permit AEC00/39W/V10 and Tasmanian Parks and Wildlife Service permit number FA 02185. I would like to thank the numerous field assistants who contributed to the collection of data during the field season. I would like to acknowledge the assistance of R. Purdon from the Tasmanian Wildlife Service. This manuscript was improved with comments from the anonymous referees.

REFERENCES

- BALDWIN, S.P., OBERHOLSER, H.C. & WORLEY, L.G. 1931. Measurements of birds. Scientific Publication of Cleveland Museum of Natural History 2: 1–167.
- BIRDLIFE INTERNATIONAL 2013. Species factsheet: *Larus pacificus*. [Available online at http://www.birdlife.org; accessed 24 April 2013].
- BITTINGER, M.L. 1996. *Calculus and its Application*. New York: Addison-Wesley Publishing Company.
- BOLTON, M., HOUSTON, D.C. & MONAGHAN, P. 1992. Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. *Journal of Animal Ecology* 61: 521–532.
- BOLTON, M., MONAGHAN, P. & HOUSTON, D.C. 1993. Proximate determination of clutch size in lesser black-backed gulls: the roles of food supply and body condition. *Canadian Journal of Zoology* 71: 273–279.
- BROWN, R.G.B. 1967. Breeding success and population growth of Herring and Lesser Black-backed Gulls *Larus argentatus* and *L. fuscus. Ibis* 109: 502–515.
- BROTHERS, N., PEMBERTON, D., GALES, R. & SKIRA, I. 1996. The status of seabirds in Tasmania. In Ross, G., Weaver, K. & Greig, J. (Eds). *The Status of Australia's Seabirds*. Canberra: Biodiversity Group, Environment Australia. pp. 181–183.
- BROTHERS, N., PEMBERTON, D., PRYOR, H. & HALLEY, V. 2001. *Tasmania's Offshore Islands: Seabirds and Other Natural Features*. Hobart: Tasmanian Museum and Art Gallery.
- BURBIDGE, A.A. & FULLER P.J. 1989. Numbers of breeding seabirds on Pelsaert Island, Houtman Abrolhos, Western Australia. *Corella* 13: 57–61.
- BURBIDGE, A.A. & FULLER, P.J. 2004. Numbers of nonburrowing breeding seabirds of the Houtman Abrolhos: 1991– 1993 and 1999. *Corella* 28: 96–103.
- COULSON, R. & COULSON, G. 1993. Diets of the Pacific gull *Larus pacificus* and the kelp gull *Larus dominicanus* in Tasmania. *Emu* 93: 50–53.
- COULSON, R. & COULSON, G. 1998. Population change among Pacific, kelp and silver gulls using natural and artificial feeding sites in south-eastern Tasmania. *Wildlife Research* 25: 183–198.
- COULSON, J.C., POTTS, G.R. & HOROBIN, J. 1969. Variation in the eggs of the shag (*Phalacrocorax aristotelis*). Auk 86: 232–245.
- COULTER, M.C. 1980. Limits to egg size in the Western Gull, Larus occidentalis. Journal of Field Ornithology 51: 75–77.
- DAVIS, J.W.F. & DUNN, E.K. 1976. Intraspecific predation and colonial breeding in Lesser Black-backed Gulls *Larus fuscus*. *Ibis* 118: 65–71.
- FISHER, J. & LOCKLEY, R.M. 1989. *Seabirds*. London: Bloomsbury Books.
- FORDHAM, R.A. 1964. Breeding biology of the Southern Blackbacked Gull: II Incubation and the chick stage. *Notornis* 11: 110–126.

- FULLER, P.J., BURBIDGE, A.A. & OWENS, R. 1994. Breeding seabirds of the Houtman Abrolhos, Western Australia: 1991– 1993. Corella 18: 97–113
- FURNESS, R.W. & MONGHAN, P. 1987. *Seabird Ecology*. Glasgow: Blackie.
- HARRIS, S., BUCHANAN, A. & CONNOLY, A. 2001. One Hundred Islands: The Flora of the Outer Furneaux. Hobart: Tasmanian Printing Authority.
- HARRIS, M.P. & WANLESS, S. 1997. Breeding success, diet and brood neglect in the kittiwake (*Rissa tridactyla*) over an 11-year period. *ICES Journal of Marine Science* 54: 615–623.
- HAYCOCK, K.A. & THRELFALL, W. 1975. The breeding biology of the Herring Gull in Newfoundland. *Auk* 92: 678–697.
- HIGGINS, P.J. & DAVIES, S.J.J.F. (Eds.) 1996. Handbook of Australian, New Zealand and Antarctic Birds. Volume 3: Snipe to Pigeons. Melbourne: Oxford University Press.
- HOLLOWAY, B.P. 2001. The reproductive biology of the Pacific Gull, Larus pacificus, breeding in loose pairs and colonies in the Furneaux Group, Tasmania. Honours Thesis. Wodonga, Australia: La Trobe University.
- KADLEC, J.A., DRURY, W.H. & ONION, D.K. 1969. Growth and mortality of Herring Gull chicks. *Bird Banding* 40: 222–233.
- KILPI, M., HILLSTRÖM, L. & LINDSTRÖM, K. 1996. Egg-size variation and reproductive success in the Herring Gull *Larus* argentatus: adaptive or constrained egg size of the last egg? *Ibis* 138: 212–217.
- KING, J.R. 1973. Energetics of reproduction in birds. In: Farner, D.S. (Ed.) *Breeding Biology of Birds*. Washington, DC: National Academy of Science. pp. 77–107.
- LACK, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- LAMONT, C. 2004. Sex allocation and reproductive costs in a gull with a long breeding season. PhD Thesis. Perth, Australia: Murdoch University.
- LINDSAY, M.C.M. & MEATHREL, C.E. 2008. Where, when and how? Limitations of the techniques used to examine the dietary preference of Pacific Gulls (Larus pacificus) using nonconsumed parts of prey and regurgitated pellets of prey remains. *Waterbirds* 31: 611–619.
- MCGILL, A.R. 1943. Probable occurrence of the southern blackbacked gull (*Larus dominicanus*) in Australia. *Emu* 43: 65–66.
- MEATHREL, C.E. 1991. The reproductive performance and body condition of Silver Gulls *Larus novaehollandiae* during a protracted breeding season. PhD Thesis. Perth, Australia: Murdoch University.
- MEATHREL, C.E. & RYDER, J.P. 1987 Intraclutch variation in the size, mass and composition of Ring-billed Gull eggs. *Condor* 89: 364–368.
- MEATHREL, C.E., RYDER, J.P. & TERMAAT, B.M. 1987. Size and composition of Herring Gull eggs: relationship to position in the laying sequence and the body condition of females. *Colonial Waterbirds* 10: 55–63.
- MILLS, J.A. 1979. Factors affecting the egg size of Red-billed Gulls *Larus novaehollandiae scopulinus*. *Ibis* 121: 53–67.
- MILLS, J.A. 1989. Red-billed Gulls. In: Newton, I. (Ed.) Lifetime Reproduction in Birds. London: Academic Press. pp. 387–404.

- MILLS, J.A. & SHAW, P.W. 1980. The influence of age on laying date, clutch size and egg size of the white-fronted tern, *Sterna striata. New Zealand Journal of Zoology* 7: 147–153.
- MINEAU, P., SMITH, G.E.J., MARKEL, R. & LAM, C-S. 1982. Aging Herring Gulls from hatching to fledging. *Journal of Field Ornithology* 53: 394–402.
- NAWROCKI, P. 1989. Determining the sequence of egg laying in clutches of Common Gull based on eggshell pattern. *Notatki Ornitologiczne* 30: 73–77.
- NISBET, I.C.T., HATFIELD, J.S., LINK, W.A. & SPENDELOW, J.A. 1999. Predicting chick survival and productivity of Roseate Terns from data on early growth. *Waterbirds* 22: 90–97.
- PARSONS, J. 1970. Relationship between egg size and posthatching chick mortality in the herring gull (*Larus argentatus*). *Nature* 228: 1221–1222.
- PARSONS, J. 1975. Seasonal variation in the breeding success of the herring gull: an experimental approach to pre-fledging. *Journal of Animal Ecology* 44: 553–573.
- PARSONS, J. 1976. Factors determining the number and size of eggs laid by the Herring Gull. *Condor* 78: 481–492.
- PAYNTER, R.A.J. 1949. Clutch size and the egg and chick mortality of Kent Island herring gulls. *Ecology* 30: 146–166.
- REED, L.M., CACCAMISE, D.F. & ORRELL, E.P. 1998. Aging of Laughing Gull nestlings using head-bill length. *Colonial Waterbirds* 21: 414–417.
- REID, W.V. 1987. The cost of reproduction in the Glaucous-winged Gull. *Oecologia* 74: 458–467.
- REID, W.V. 1988. Age-specific patterns of reproduction in the glaucous-winged gull: increased effort with age? *Ecology* 69: 1454–1465.
- RICKLEFS, R.E. 1968. Pattern of growth in birds. *Ibis* 110: 419–450.
- RISCH, T.S. & ROHWER, F.C. 2000. Effects of parental quality and egg size on growth and survival of herring gull chicks. *Canadian Journal of Zoology* 78: 967–973.
- SANCHEZ-GUZMÁN, J.M. & MUŇOZ DEL VIEJO, A. 1998. A method for age determination for nestling Gull-billed Terns. *Colonial Waterbirds* 21: 427–430.
- SURMAN, C.A. & NICHOLSON, L.W. 2009. A survey of the breeding seabirds and migratory shorebirds of the Houtman Abrolhos, Western Australia. *Corella* 33(4):89–98.
- SERVENTY, D.L., SERVENTY, V.N. & WARHAM, J. 1971. Handbook of Australian Seabirds. Melbourne: Reed.
- SOKAL, R.R. & ROHLF, F.J. 1995. Biometry, 3rd Ed. New York: Freeman.
- SPSS INC. 2003. SPSS for Windows. Chicago: SPSS Corp.
- SYDEMAN, W.J. & EMSLIE, S.D. 1992. Effects of parental age on hatching asynchrony, egg size and third-chick disadvantage in Western Gulls. *Auk* 109: 242–248.
- WOOLLER, R.D. & DUNLOP, J.N. 1979. Multiple laying by the silver gull, *Larus novaehollandiae* Stephens, on Carnac Island, Western Australia. *Australian Wildlife Research* 6: 325–335.
- YORIO, P., BERTELLOTTI, M. & QUINTANA, F. 1995. Preference for covered nest sites and breeding success by Kelp Gulls *Larus dominicanus*. *Marine Ornithology* 23: 121–128.