Effects of clutch size and egg-laying order on the breeding success in the Little Tern *Sterna albifrons* on the Nakdong Estuary, Republic of Korea

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Survivorship of Little Tern *Sterna albifrons* eggs and chicks was followed on an islet in the Nakdong Estuary, Republic of Korea, in 1995 and 1996. Mean egg size and incubation period were significantly different between the 2 years. The maximum clutch size was three eggs, and the second egg in the clutch often hatched earlier than the first, while most of the third eggs hatched last. In 1996, when the fate of 249 eggs from 106 nests was followed for 40 days, hatching success, fledging success and breeding success were 77%, 40% and 31%, respectively. High mortality occurred in the early chick stage, mostly because of rain and predation by Weasels *Mustela sibirica*. The breeding success per egg was 14% in one-egg clutches, 28% in two-egg clutches and 34% in three-egg clutches. This difference was mainly attributed to the lower hatching success in the smaller clutches. In three-egg clutches, the third egg showed significantly lower breeding success than siblings. The main foods of the Little Tern were *Tridentiger obscurus*, *Engraulis japonicus*, *Hyporhamphus intermedius*, *Acanthogobius flavimanus* (all fish), *Palaemon* sp. and *Crangon affinis* (shrimps). The feeding frequency was, apparently, not affected by time of day and age of chicks but was probably influenced by weather conditions. Newly hatched chicks failed to eat 25% of the prey brought to them, although this decreased with the age of the chicks.

The Little Tern *Sterna albifrons* is widespread throughout the world, breeding in every continent other than Antarctica (Lloyd *et al.* 1975). However, this species has been decreasing, especially in Australia (Morris 1979, Clancy 1987), Britain and Ireland (Parslow 1967, Lloyd *et al.* 1975) and Japan (Hayasi & Okada 1992, Toba 1994), as a result of the increased human disturbance on sandy coasts where they breed. Studies on this species have examined distribution (Norman & Saunders 1969), yearly fluctuation of number in colonies (Parslow 1967, Lloyd *et al.* 1975), interbreeding of subspecies (Cox & Close 1977), egg and chick recognition (Saino & Fasola 1993) and chick adoption (Saino *et al.* 1994). Although studies of breeding success and mortality factors, which are necessarily required for planning the conservation of bird species, have been conducted in southeastern India (Holloway 1993), Australia (Vincent 1983, Larkins 1984, Clancy 1987) and Britain and Ireland (Davies 1981), the mortality factors vary between regions and there are few data on the breeding success of Little Terns which breed in Korea, Japan and China and overwinter in the Philippines, New Guinea and Australia (Core & Won 1971, Higgins & Davies 1996). The aims of the present study were to determine the breeding success, the cause of egg and chick mortality and the feeding activities of Little Terns, with special reference to the effects of clutch size and egg-laying order on the hatching, fledging and overall breeding successes.

STUDY SITE AND METHODS

The Nakdong Estuary (35°15′N, 128°54′E, Fig. 1) contains some islets where Little Terns breed in large numbers. This study was conducted on the 3.5 km long and 0.3 km wide Sinja-Do Islet, which is sparsely covered by reeds and sedges such as *Phragmites communis*, *Scirpus triqueter*, *Carex pumila*, *Cynodon dactylon*, and *Carex scabrifolia* (Kim *et al.* 1981, Yoon 1991). Strong winds often blow from the open sea, and waves occasionally run well up the south beach, while the north beach is sometimes flooded at high tide. During the breeding season, the highest tide occurred on 15 May (incubation season) in 1995 and on 3 June (chick period) in 1996. Although mammals are rare on this islet, a few Weasels *Mustela sibirica* from nearby Jangja-Do Islet sometimes visited during low tide, when the two islets are connected by a temporary land bridge.

Nest census and preliminary survey of survivorship in 1995

From 22 April to 12 July 1995, nest counts were made by visiting the whole islet almost daily. Whenever an adult bird laid eggs and started incubation, the nest was followed for about 24 days until all of the eggs had hatched. We measured the length and width of 259 eggs and calculated their shape index and volume. Egg size was measured to the near-

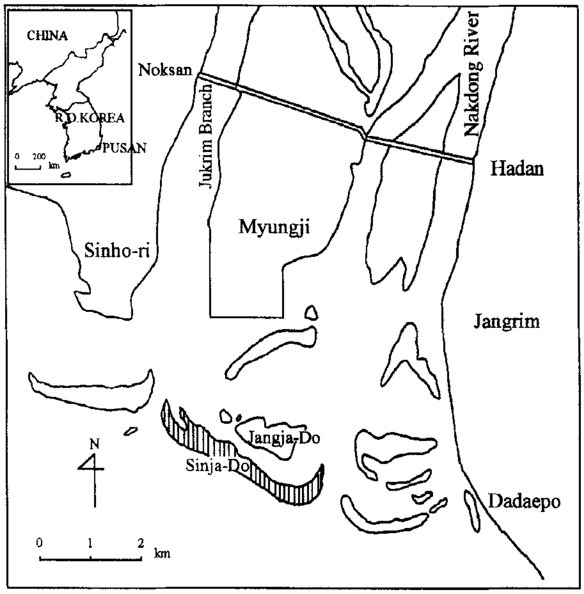

Figure 1. Location of the Little Tern study site, Sinja-Do (shaded) Islet on Nakdong Estuary, Pusan.

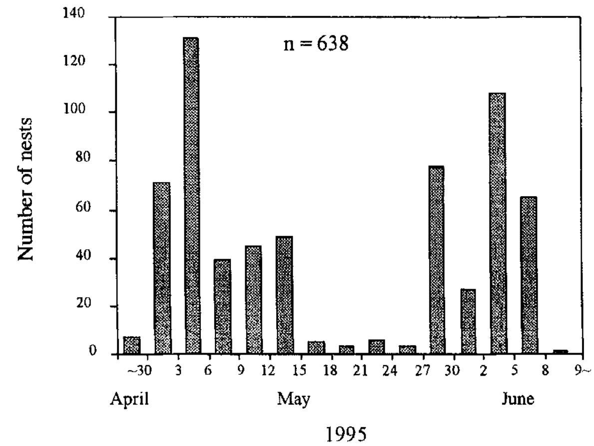

Figure 2. Seasonal trend of Little Tern nests in 1995. A nest was regarded as founded when an adult laid the first egg.

est ± 0.1 mm with Vernier calipers, and the egg volume (V) was calculated by $V = K \times L \times B^2 / 1000$, where K is a constant and L and B are length and breadth of egg, respectively (cf. Hoty 1979). In this study, we used K = 0.4866 as calculated for the Kittiwake *Rissa tridactyla*, and the shape index (SI) was given by $B \times 100/L$ (Coulson 1963).

Prior to hatching, 30 nests with eggs were each enclosed within a 40-cm-high × 520-cm-long nylon net fence (mesh size, 1.67 mm × 1.99 mm) to retain the chicks. After the eggs hatched, the chicks were counted daily for 14 days and the cause of any mortality was determined. The following mortality factors involving eggs and chicks were recognized in this study. **Predators:** eggs and chicks were taken by Weasels, Brown Rats *Rattus norvegicus*, Magpies *Pica pica*, Slaty-backed Gulls *Larus schistisagus* and humans, all of which could be identified by their footprints in the sand. **Wind:** eggs were lost when covered by a thick layer of sand carried by strong winds. **Waves:** eggs were washed away by high waves, especially on the south beach of the islet. **Flood:** eggs were washed away by high tides, especially on the north beach of islet. **Abandonment:** eggs and chicks were abandoned by their parents for unknown reasons. **Starvation:** younger chicks sometimes starved during food competition with older siblings. **Rain:** during rain, young chicks, with non-waterproof down, died if not protected by their parents. **Infertile eggs:** eggs failed to hatch.

Detailed survey in 1996

From 21 April to 20 June 1996, 106 nests were chosen, and as soon as each egg was laid, it was individually marked with an indelible ink and measured for size, volume and weight. Egg size was measured to the nearest 0.01 mm with digital Vernier calipers, and egg weight was measured to the nearest 0.1 g on a digital pan balance. Prior to egg hatching, the nest area was again enclosed by a nylon net fence as used in 1995, and each chick was individually marked by ringing in order to follow its fate for 14 days. In this study, we used only the clutches in which the first or second eggs or both survived at least 3 days, so that time existed for a third egg to be laid. Three days was the longest interval found between laying successive eggs in the present study.

Observation of feeding behaviour and food in 1996

In the 1996 breeding season, the feeding frequency was recorded at each of nine nests with chicks from 07.30 h to 19.30 h on 1 day each. The brood age, i.e. days after the last chick hatched in each clutch, ranged from 1 to 14 days. Three of the nine nests were observed on rainy days, while the other six nests were observed on fine days. Effects of time, brood age and weather on the feeding frequency were examined by ANOVA.

Chicks sometimes failed to eat prey presented by the parents. In 1995 and 1996, the food habit of this bird species was estimated from these abandoned prey.

Terminology

Hatching success, fledging success and breeding success were calculated as H/T, C/H and C/T, respectively, where T is the total number of eggs laid, H is the number of eggs hatched, and C is the number of chicks which survived for 14 days or more. Incubation period was the number of days from the laying of the last egg to the hatching of the last chick and unhatched eggs were not considered.

Means are shown with standard deviations. Clutches with one, two and three eggs are abbreviated to c/1, c/2 and c/3, respectively.

Table 1. *Clutch size of Little Terns at Sinja-Do Islet based on 638 nests in 1995 and 106 nests in 1996*

Clutch size	1995 No.	1995 %		1996 No.	1996 %
c/1	31	5		11	10
c/2	269	42		47	44
c/3	338	53		48	45
Mean	2.48			2.35	
s.d.	0.59			0.66	
G-test			n.s.		

RESULTS

Clutch size and egg size

In 1995, 638 nests were found on Sinja-Do Islet (125 ha), with a density of 5.1 nests per ha. Eggs were laid from 28 April to 16 June, with peaks in early May and early June (Fig. 2). This bimodality probably occurred because some unsuccessful birds laid again in late May or early June.

The mean clutch sizes were 2.48 ± 0.59 eggs for 638 nests in 1995 and 2.35 ± 0.66 eggs for 106 nests in 1996 (Table 1). The mean clutch size did not differ significantly between the 2 years (G_2 = 5.19, n.s.). The mean sizes of eggs in 1995 and 1996 were, respectively, 32.3 ± 1.1 mm and 31.72 ± 1.22 mm for length, 24.3 ± 0.6 mm and 23.81 ± 0.63 mm for breadth, 9.24 ± 0.59 cm^3 and 8.76 ± 0.61cm^3 for volume and 75.16 ± 3.29 and 75.27 ± 2.89 for shape index. All of the between-year differences were statistically significant ($P < 0.001$), except for shape index.

The analysis of egg measurements in the laying sequence showed that much of the variation in egg size was a consequence of egg-laying order (Table 2). In c/2 (n = 47), one-way ANOVA showed that the size differences between the first and second egg were not statistically significant for length or shape index but were significant for volume ($F_{1,92}$ = 4.6, $P < 0.05$) and weight ($F_{1,92}$ = 7.7, $P < 0.001$). In c/3 (n = 48), no significant difference in length of the three eggs was found, but significant differences existed in breadth ($F_{2,141}$ = 12.8, $P < 0.001$), volume ($F_{2,141}$ = 8.2, $P <$ 0.001), shape index ($F_{2,141}$ = 6.6, $P < 0.002$) and weight ($F_{2,141}$ = 7.7, $P < 0.001$). Table 2 indicates that egg size declined with laying sequence.

Incubation period

The incubation period was determined for 52 nests in 1995 and for 66 nests in 1996. In c/2 and c/3, the egg-laying interval was 1 to 3 days between the first and second eggs and between the second and third eggs. A clutch was incubated for 17–25 days until all eggs hatched. The mean (±s.d.) incubation periods were 19.8 ± 1.3 days in 1995 (n = 52 nests) and 20.8 ± 1.1 days in 1996 (n = 66). The between-year difference is statistically significant (t_{116} = 4.37, $P < 0.001$), probably because the cloudy or rainy days were more frequent and the mean temperature was lower in 1996 than in 1995.

The eggs in a clutch hatched synchronously, i.e. within a day, in 17 (33%) of 52 nests and in 30 (46%) of 66 nests. In the other nests, the eggs hatched asynchronously, taking up to 4 days to complete the hatching of all eggs. In 1996, the correlation between egg-laying order and hatching order was determined for 35 clutches where all three eggs hatched. The mean (±s.d.) hatching order was 1.51 ± 0.56 days for the first-laid eggs, 1.54 ± 0.56 days for the second laid and 2.94 ± 0.24 days for the third laid, so that whilst the third egg was almost always the last to hatch, incubation of the first and second eggs seemed to start at the same time, resulting in either egg hatching first.

Survival of eggs and chicks

In 1996, 249 eggs were laid in 106 nests and were followed for 40 days (Fig. 3). The hatching success was 76.7% (191/249), fledging success 39.8% (76/191) and breeding success 30.5% (76/249). The mortality rate was highest between days 20–28, i.e. over the hatching stage, and reached 40% (102/249), i.e. 59% (102/173) of the total mortality. The main mortality factors were predators, wind and wave action for eggs and predators, rain and starvation for chicks, although a flood caused appreciable losses of eggs in 1995 (Table 3) when the highest tide occurred during the incu-

Table 2. *Mean egg size (±s.d.) of Little Terns according to egg-laying order in two- and three-egg clutches in 1996*

	Two-egg clutch (n = 47)			Three-egg clutch (n = 48)			
	No. 1 egg	No. 2 egg	P	No. 1 egg	No. 2 egg	No. 3 egg	P
Mean length (mm)							
Mean breadth (mm)	32.19 ± 1.33	31.70 ± 1.33	n.s.	31.80 ± 1.14	31.26 ± 1.15	31.50 ± 1.05	n.s.
Mean volume (cc)	23.96 ± 0.64	23.74 ± 0.71	n.s.	23.91 ± 0.53	23.97 ± 0.54	23.46 ± 0.55	<0.001
Shape index	9.00 ± 0.61	8.71 ± 0.72	<0.05	8.86 ± 0.54	8.74 ± 0.49	8.44 ± 0.52	<0.001
Mean mass (g)	74.57 ± 3.69	74.99 ± 3.09	n.s.	75.29 ± 2.93	76.78 ± 3.44	74.54 ± 2.83	<0.01
	9.82 ± 0.72	9.50 ± 0.84	<0.001	9.66 ± 0.62	9.57 ± 0.54	9.22 ± 0.56	<0.001

Table 3. *Mortality of eggs and chicks of Little Terns at Sinja-Do Islet*

	1995		1996	
	Eggs	Chicks	Eggs	Chicks
Observed (*n*)	1583	81	249	191
Mortality factors (%)				
Predators	6.2	50.6	6.0	33.5
Wind	12.3	—	2.8	—
Wave	9.0	—	2.0	—
Flooded	15.5	—	—	—
Abandoned	0.9	4.9	7.2	—
Starved	—	4.9	—	6.8
Rain	—	3.7	—	8.4
Infertile eggs	1.1	—	4.4	—
Others or unknown	0.4	—	0.8	11.5
Total	45.5	64.2	23.3	60.2

bation season. Newly hatched chicks were vulnerable to rain. The high mortality in the hatching stage was caused mainly by rain and Weasels; the Weasels preferred chicks to eggs.

Effects of clutch size and egg-laying order on the survival of eggs and chicks were analysed for 106 nests (Table 4). Totals of 7, 94 and 144 eggs were laid in c/1, c/2 and c/3, and the breeding successes were 14%, 28% and 34%, respectively. This difference was mostly a result of the low hatching success in single-egg clutches: 43% in c/1, 72% in c/2 and 83% in c/3 (Table 4). The difference in hatching success between c/1, c/2 and c/3 was statistically significant ($G_2 = 7.77$, $P < 0.05$), but fledging success was not significantly different.

In c/2 and c/3, first and second eggs were not significantly different in hatching success, fledging success and breeding success (Table 3). However, the successes of the second and third eggs in c/3 were significantly different ($G_1 = 3.98$, $P < 0.05$), indicating a disadvantage for the last-laid egg in a clutch. The breeding success arising from second eggs was 40% but it was only 21% in the third eggs.

Food and feeding activity

Totals of 197 and 643 food items belonging to 17 and 21 species were collected and identified in 1995 and 1996, respectively. The following species were abundant in both years: fish (*Tridentiger obscurus, Engraulis japonicus, Hyporhamphus intermedius* and *Acanthogobius flavimanus*) and shrimps (*Palaemon* sp. and *Crangon affinis*) (Table 5).

Table 6 shows the feeding frequency at intervals of 2 h from 07.30 h to 19.30 h in nine nests which were at different age stages when they were observed on fine days (six nests, I–VI) or cloudy-rainy days (three nests, VII–IX). Two-way ANOVA for the six nests I–VI indicated that the time of day and age did not significantly affect the feeding frequency. However, three-way ANOVA for a pair of three nests (IV–VI and VII–IX) suggested a significant effect of weather condition on the feeding frequency ($F_{1,27} = 11.9$, $P < 0.02$), with parents bringing an average ($\pm$sd) of 11.4 ± 7.8 prey per h on fine days but only $5.x7 \pm 3.1$ on cloudy or rainy days. When given food by parents, the chicks sometimes

Table 4. *Hatching success, fledging success and breeding success of Little Terns at Sinja-Do Islet in 1996*

	1996									
	Hatching success			Fledging success			Breeding success			
Clutch size	No. laid		No. hatched	No. hatched		No. fledged	No. laid		No. fledged	% fledged
c/1 (7)[a]	7		3	3		1	7		1	14
c/2 (47)										
First egg	47		34	34		13	47		13	28
G-test		n.s.			n.s.			n.s.		
Second egg	47		34	34		13	47		13	28
Total	94		68	68		26	94		26	28
c/3 (48)										
First egg	48		40	40		20	48		20	42
G-test		n.s.			n.s.			n.s.		
Second egg	48		42	42		19	48		19	40
G-test		n.s.			n.s.			$P < 0.05$		
Third egg	48		38	38		10	48		10	21
Total	144		120	120		49	144		49	34

[a] Out of 11 eggs (cf. Table 1), four eggs died within the age of 3 days.

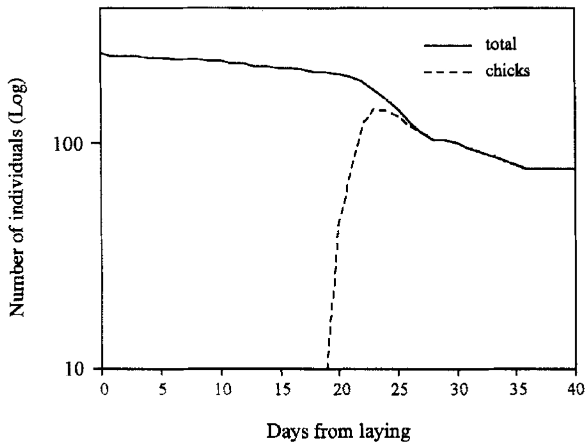

Figure 3. Survivorship curve of Little Terns during 40 days in 1996. Initial number of eggs was 249. The increase of chicks is shown by a broken line.

failed to eat it. Some food seemed too large for chicks to eat, but even food which was not too large was occasionally discarded. As shown in Figure 4, the feeding failure most often occurred with young chicks. At nests I and II, the newly hatched chicks failed to eat 25% of prey brought to them, whilst all food was consumed in nests VI, VIII and IX, which had chicks over 9 days old.

DISCUSSION

Little Terns breed solitarily or colonially (Lloyd *et al.* 1975, Cramp 1985, Higgins & Davies 1996). Colonial breeding is considered more successful against predatory birds such as Brahminy Kite *Hariastur indus*, Osprey *Pandion haliaetus*, Brown Falcon *Falco berigora*, Kestrel *Falco tinnunculus*, Silver Gull *Larus novaehollandiae*, Kelp Gull *Larus dominicanus*, Pacific Gull *Larus pacificus*, Gull-billed Tern *Gelochelidon nilotica*, Australian Magpie *Gymnorhina tibicen* and Torresian Crow *Corvax orru*, which are all diurnal and which often encounter communal defence (Wiklund & Andersson 1980, Davies

Table 5. *Food brought to Little Tern chicks*

Prey species	1995		1996	
	n	%	*n*	%
Fish				
Acanthogobius flavimanus	8	4.1	103	16.0
Acheilognathus rhombeus	5	2.5	7	1.1
Apocryptodon punctatus			3	0.5
Carassius auratus	1	0.5	8	1.2
Coilia ectenes	1	0.5	3	0.5
Engraulis japonicus	21	10.7	16	2.5
Etrumeus teres	1	0.5		
Gasterosteus aculeatus	1	0.5		
Hyporhamphus intermedius	9	4.6	15	2.3
Lateolabrax japonicus			10	1.6
Leiognathus nuchalis			8	1.2
Mugil cephalus	5	2.5	10	1.6
Plecoglossus altivelis altivelis			1	0.2
Pleuronectes yokohamae			3	0.5
Pseudoblennius cottoides			5	0.8
Pseudorasbora parva			1	0.2
Pungitius sinensis	1	0.5		
Sardinella zunasi			6	0.9
Sillago japonica	1	0.5		
Trachurus japonicus	5	2.5	58	9.0
Tridentiger obscurus	51	25.9	125	19.4
Zoarchias veneficus			2	0.3
Parioglossus sp.	5	2.5	9	1.4
Unidentified species	12	6.1		
Shrimps				
Crangon affinis	38	19.3	87	13.5
Palaemon sp.	32	16.2	163	25.3
Total	197	100	643	100

Table 6. *Feeding frequency of Little Tern chicks in relation to time of day, age and weather in 1996*

Weather	Nest code	Days since last hatch	Hours 07.30	09.30	11.30	13.30	15.30	17.30	19.30	Mean no. ± s.d.	Total prey
Fine	I	1	4	8	6	10	16	6		8.33 ± 4.27	50
	II	2	6	5	16	16	5	10		9.67 ± 5.24	58
	III	3	5	9	3	8	17	13		9.17 ± 5.15	55
	IV	5	16	7	8	19	14	4		11.33 ± 5.85	68
	V	10	11	15	17	4	9	8		10.67 ± 4.76	64
	VI	14	12	9	45	10	26	15		19.5 ± 13.92	117
Mean			9	8.83	15.83	11.17	14.5	9.33		11.44 ± 7.78	
s.d.			4.73	3.37	15.33	5.46	7.23	4.18			
Cloudy and rainy	VII	5	3	7	10	5	4	9		6.33 ± 2.80	38
	VIII	10	5	5	7	11	9	7		7.33 ± 2.34	44
	IX	14	2	7	6	0	4	1		3.33 ± 2.80	20
Mean			3.33	6.33	7.67	5.33	5.67	5.67		5.67 ± 3.05	
s.d.			1.53	1.15	2.08	5.51	2.89	4.16			

1981). When birds in a colony were attacked by nocturnal predators such as Little Owls *Athene noctua* in England (Norman & Saunders 1969) and Short-eared Owls *Asio flammeus* in Britain and Ireland (Lloyd *et al.* 1975), communal defence rarely occurred. Therefore, colonial breeding may not always be more advantageous than solitary breeding. On our study site, owls were absent in spring and summer, and the effective nocturnal predators were Weasels, which came from a neighbouring islet only occasionally. This low density of nocturnal predators probably enabled the Little Terns to form a dense colony of nests on Sinja-Do Islet, which is located in the food-rich Nakdong Estuary. Although flooding at high tide sometimes caused the loss of eggs (Norman & Saunders 1969, Burger & Lesser 1978, Clancy 1987, Blomqvist & Johansson 1995), this mortality factor does not always occur and probably is not enough to reduce the advantage of colonial breeding.

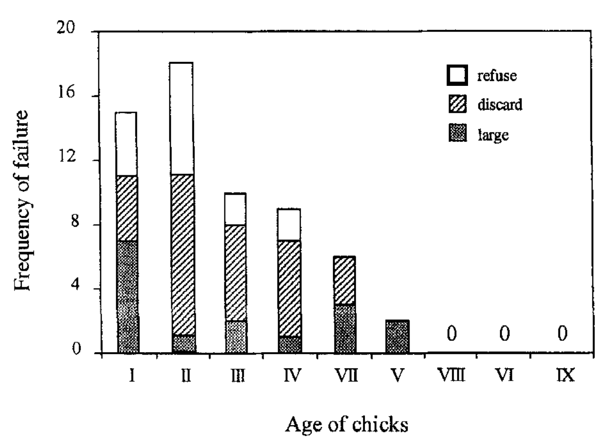

Figure 4. Frequency of feeding failure in nine Little Tern nests. Large: the given prey was too large for the chick to eat; discard: the prey was not large but the chick discarded it soon after received; refuse: the chick refused to receive the prey.

Although the clutch size in each nest is often dependent on the age of parents, with younger parents laying smaller number of eggs (Coulson 1966, Klomp 1970, Coulson & Porter 1985), the mean clutch size in the Little Tern seems to be more affected by the food condition of the habitat (Klomp 1970, Custer *et al.* 1996). The mean clutch sizes of 2.48 eggs in 1995 and 2.35 eggs in 1996 were markedly larger than 2.05 eggs in southeast India (Holloway 1993), or 2.09 (Clancy 1987) and 2.32 eggs (Larkins 1984) in New South Wales, Australia.

In many bird species, the egg-laying order and the hatching order affect the survivorship of chicks (Parsons 1975, Howe 1976, Furness 1983, Bolton 1991). For instance, in the Herring Gull *Larus argentatus* and Western Gull *Larus occidentalis*, the third egg is smaller than the first and second eggs, and the chick which emerges from the third egg suffers much higher mortality than either of its siblings (Parsons 1970, 1975, Langham 1972, Sydeman & Emslie 1992). The present study has also shown that the third egg of the Little Tern is significantly smaller than the other two eggs and that its success to hatching and fledging is distinctly low, probably because the chicks from the small eggs are vulnerable to starvation (Davies 1981) and disadvantaged in the food competition among siblings (Young 1963, Lundberg & Väisänen 1979, Davies 1981, Hahn 1981). It seems likely that the third eggs are supplementary to the reproductive success and the third chick survives only when the habitat conditions are favourable (Langham 1972, Davies 1981). The first 2 or 3 days after hatching are critical for the survival of chicks (Davies 1981 and this study). Probably because of the low density of predators and the abundance of food, all three chicks did survive for 14 days or more in 8 of 48 three-egg clutches in our study, whereas Davies (1981) reported that, at Gibraltar Point, Lincolnshire, there were no nests where all three chicks successfully fledged. The number of successfully fledged chicks per nest at Sinja-Do Islet was 0.72 (76/106), which is much larger than the 0.16 chick per nest found in New South Wales, Australia (Larkins 1984) and 0.24 chick per nest in southeast India (Holloway 1993).

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REFERENCES

Blomqvist, D. & Johansson, O.C. 1995. Trade-offs in nest site selection in coastal populations of Lapwings *Vanellus vanellus*. Ibis 137: 550–558.

Bolton, M. 1991. Determinants of chick survival in the Lesser Black-Backed Gull: Relative contributions of egg size and parental quality. J. Anim. Ecol. 60: 949–960.

Burger, J. & Lesser, F. 1978. Selection of colony sites and nest sites by Common Terns *Sterna hirundo* in Ocean County, New Jersey. Ibis 120: 433–449.

Clancy, G.P. 1987. The breeding status of the Little Tern *Sterna albifrons* on the South Wales North Coast, 1979 to 1982. Corella 11: 59–64.

Core, M.E.J. & Won, P.O. 1971. The birds of Korea. Seoul: Royal Asiatic Society.

Coulson, J.C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. Proc. Zool. Soc. Lond. 140: 211–227.

Coulson, J.C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. J. Anim. Ecol. 35: 269–279.

Coulson, J.C. & Porter, J.M. 1985. Reproductive success of the Kittiwake *Rissa tridactyla*: The roles of clutch size, chick growth rates and parental quality. Ibis 127: 450–466.

Cox, J.B. & Close, D.H. 1977. Interbreeding of Little and Fairy Terns. Emu 77: 28–32.

Cramp, S. 1985. The Birds of the Western Paleartic, Vol. 4. Oxford: Oxford University Press.

Custer, T.W., Hines, R.K. & Custer, C.M. 1996. Nest initiation and clutch size of Great Blue Herons on the Mississippi River in relation to the 1993 flood. Condor 98: 181–188.

Davies, S. 1981. Development and behaviour of Little Tern chicks. Br. Birds 74: 291–298.

Furness, R.W. 1983. Variations in size and growth of Great Skua *Catharacta skua* chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. J. Zool. Lond. 199: 101–116.

Hahn, D.C. 1981. Asynchronous hatching in the Laughing Gull: Cutting losses and reducing rivalry. Anim. Behav. 29: 421–427.

Hayasi, H. & Okada, T. 1992. The breeding status of the Little Tern *Sterna albifrons* in Japan. Strix 11: 157–168 [In Japanese with English summary].

Higgins, P.J. & Davies, S.J.J.F. 1996. Handbook of Australian, New Zealand and Antarctic Birds, Vol. 3. Oxford: Oxford University Press.

Holloway, M. 1993. The variable breeding success of the Little Tern *Sterna albifrons* in South-east India and protective measures needed for its conservation. Biol. Conserv. 65: 1–8.

Howe, H.F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. Ecology 57: 1195–1207.

Hoty, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96: 73–77.

Kim, J.H., Kim, H.S., Lee, I.K. & Kim, J.W. 1981. Studies on the estuarine ecosystem of Nagdong River. Seoul Natl. Univ. Res. Inst. Bas. Sci. 1–84. [In Korean].

Klomp, H. 1970. The determination of clutch-size in birds. Ardea 58: 1–124.

Langham, N.P.E. 1972. Chick survival in terns (*Sterna* spp.) with particular reference to the Common Tern. J. Anim. Ecol. 41: 385–395.

Larkins, D. 1984. Little Tern breeding colony on artificial site at Port Botany, New South Wales. Corella 8: 1–10.

Lloyd, C.S., Bibby, C.J. & Everett, M.J. 1975. Breeding terns in Britain and Ireland in 1969–74. Br. Birds 68: 221–237.

Lundberg, C.-A. & Väisänen, R.A. 1979. Selective correlation of egg size with chick mortality in the Black-headed Gull (*Larus ridibundus*). Condor 81: 146–156.

Morris, A.K. 1979. The declining status of the Little Tern in New South Wales. Corella 3: 105–110.

Norman, R.K & Saunders, D.R. 1969. Status of Little Tern in Great Britain and Ireland in 1967. Br. Birds 62: 4–13.

Parslow, J.L.F. 1967. Changes in status among breeding birds in Britain and Ireland. Bri. Birds 60: 177–202.

Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). Nature 228: 1221–1222.

Parsons, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull *Larus argentatus*. Ibis 117: 517–520.

Saino, N. & Fasola, M. 1993. Egg and nest recognition by two tern species (Sternidae Aves). Ethol. Ecol. and Evol. 5: 467–476.

Saino, N., Fasola, M. & Crocicchia, E. 1994. Adoption behaviour in Little and Common Terns (Aves: Sternidae): Chick benefits and parents' fitness costs. Ethology 97: 294–309.

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.

Toba, E. 1994. Decrease of the nest of the Little Tern *Sterna albifrons* along the Sai and Chikuma Rivers in the Nagano Basin, and the protection of colonies. Strix 13: 93–101 [In Japanese with English summary].

Vincent, J. 1983. The breeding status of Little Tern *Sternaalbifrons*, East Gippsland, Victoria 1977–1980. Aust. Bird Watcher 10: 35–60.

Wiklund, C.G. & Andersson, M. 1980. Nest predation selects for colonial breeding among Fieldfares *Turdus pilaris*. Ibis 122: 363–366.

Yoon, H.S. 1991. A study on vascular hydrophytes of intertidal area in Nakdong Estuary. Korean J. Ecol. 14: 63–73 [In Korean with English summary].

Young, E.C. 1963. The breeding behaviour of the South Polar Skua *Catharacta maccormicki*. Ibis 105: 203–233.

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