DAILY NEST ATTENDANCE AND BREEDING PERFORMANCE IN THE LITTLE PENGUIN *EUDYPTULA MINOR* AT PHILLIP ISLAND, AUSTRALIA

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SUMMARY

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The daily attendance patterns of Little Penguins *Eudyptula minor* were investigated for 55 nests on Phillip Island, Australia during the pre-breeding (winter), egg-laying, incubation and guard periods of the 1995/96 season. Birds were identified by transponder tags which were subcutaneously implanted between the scapulae. Males spent significantly longer in the colony (15 days) than did females (11 days) before egg laying. Both males and females remained ashore for 5.0 days over their laying period. Eggs were incubated for 35.5 days (range 31–40 days, n = 48 nests). Incubation shifts lasted 3.4 days on average and the number of foraging trips averaged 5.6 trips per bird. After hatching parents guarded their chicks for a total of 14.5 days. Successful parents started breeding earlier, had shorter incubation shifts and undertook more foraging trips than did failed birds during both incubation and chick-guard periods. The later a Little Penguin started to breed the poorer was its breeding performance.

INTRODUCTION

The onset of laying of the Little Penguin *Eudyptula minor* at Phillip Island varies from year to year between late August and mid November (Dann 1992). The cause for the variability of the date of onset of breeding is unknown although Mickelson *et al.* (1992) suggested that it may relate to the effects of changes of sea temperature in July and August. The spread of laying dates within a season also varies between three weeks and three months (Reilly & Cullen 1981).

Given this variability it might be expected that the pattern of attendance of breeding birds at their nest varies between years and within the season. Although there are some estimates of the overall period of time a bird spends ashore (Reilly & Balmford 1975, Reilly & Cullen 1981), very little information is available for the Little Penguin on the attendance of individual birds in the colony throughout the breeding cycle and differences in attendance patterns for successful and failed breeders (Williams 1995). This absence of data is due in part to the need to remove birds from their burrows to read bands (Kinsky 1960, Hodgson 1975, Reilly & Cullen 1981) which may cause undesirable disturbance to the individuals and therefore imposes limitations on the frequency with which birds in a colony can be visited (P. Dann pers. comm.). The use of new technology has overcome this problem and as described below birds can be identified in their burrows without handling them.

This paper describes observations made at Phillip Island on the daily attendance pattern of individual Little Penguins and compares the patterns of successful and failed birds during the pre-breeding, incubation and chick-guard periods. Details are given for shifts and foraging trip duration during incubation and chick-guarding.

METHODS

The attendance of birds in the colony was investigated during the 1995/96 breeding cycle at Summerland Peninsula in the south-west of Phillip Island (38º15'S, 145º30'E), Australia. The study colony was located within the area known as the Penguin Parade. Little Penguins at this site are part of a major tourist attraction where the penguins may be viewed each evening as they arrive and move up the beach. Although they are observed by some 500 000 visitors a year there is very little disturbance to the penguins since tourists cannot touch them or move around among the colonies (Dann 1992).

The 'Parade' colony contains approximately 1000 breeding pairs (P. Dann pers. comm.). The nests included in this study were from an area consisting of the foreshore between the concrete viewing stands and the sand dunes immediately inland from the old board walk area. Daily observation of 126 nests (either in natural burrows or wooden nesting boxes) started on 28 June 1995 throughout a nine-month period which covered the breeding cycle to the end of the guard period. Eggs were laid in 53 nests and two nests had a second clutch. Thus, the sample size used in the analysis was n = 55 nests unless otherwise stated in the text. Nest 21 (Figure 1) had two males involved with one female but those males were never recorded together in the same burrow. Small wooden sticks placed at the entrance of each burrow were used to indicate whether birds had entered or left burrow between visits.

All birds were weighed and sexed by bill measurement (P. Dann pers comm.) and then injected with electronic identification tags (TIRIS) on the first occasion they were observed in nests at the colony. Tags were injected between the shoulder blades (scapula) and the wound closed with surgical glue
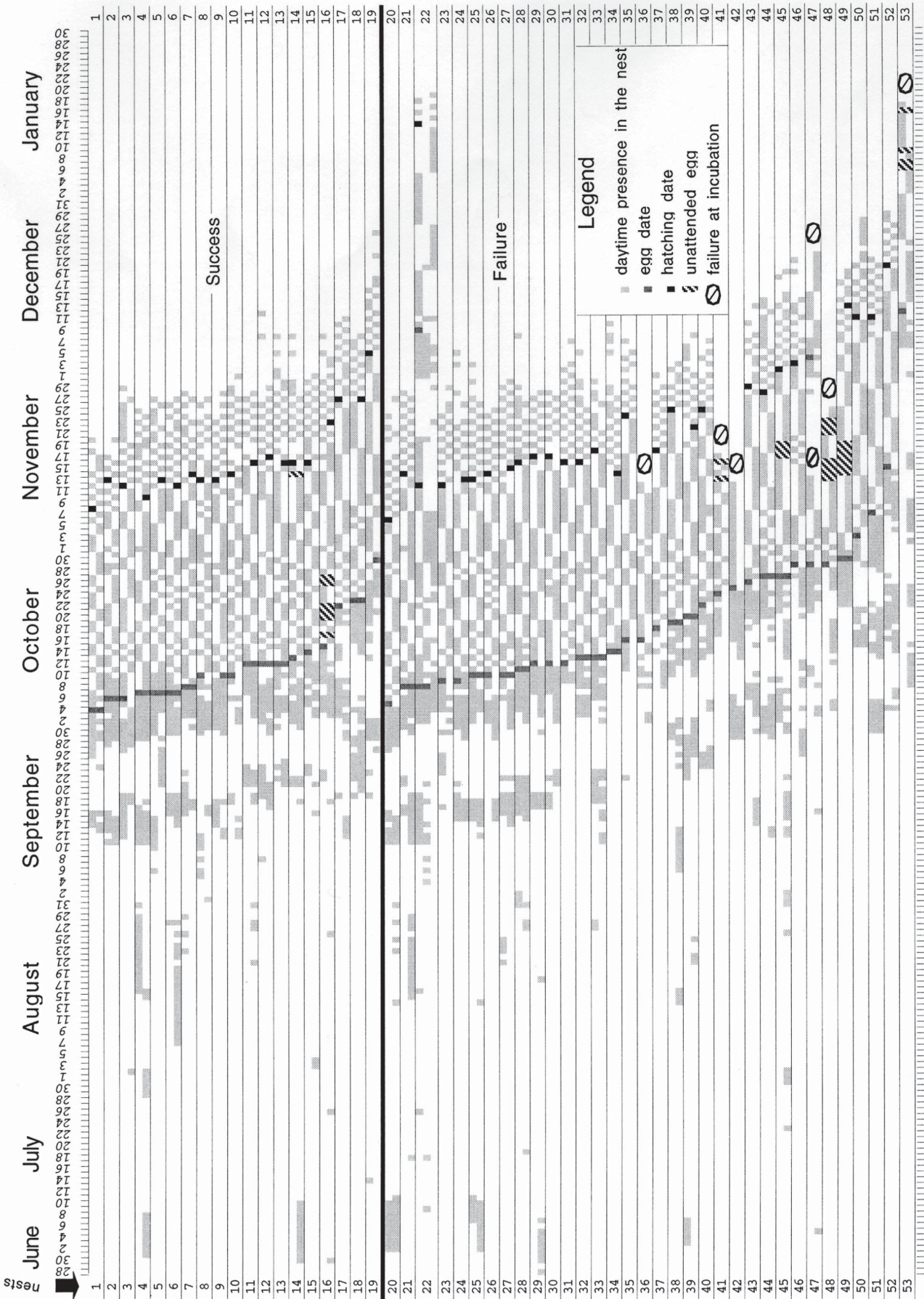
Fig. 1. *Patterns of attendance of Little Penguins from pre-egg to chick-guard periods in chronological order, 1995/96. Each row represents the attendance pattern of a pair, with the female above the male. The first 19 nests were successful, the remainder failed in their breeding attempt. See legend for details.*

(Vetbond, 3M). Unbanded birds were fitted with stainless steel flipper bands. About 75% of these birds were already banded as either chicks or as adults when they were first recaptured at the breeding colony. Because nests have been checked for unbanded birds at regular intervals since 1978 and birds return to the colony at age of two or three years (Dann & Cullen 1990) it was assumed that all adult birds were two years old at banding.

Birds arriving on the beach moved in groups into the breeding area in the sand dunes. Most birds in the study colony followed the same track and were logged by an Automated Penguin Monitoring System (APMS) developed by the Australian Antarctic Division (Kerry *et al*. 1993) which was placed on their pathway. The APMS automatically recorded the tag number, date/time and direction of the bird. Birds which followed an alternate track were logged by a simpler system which recorded tag number only. Burrows were checked each day using a hand-held reader which could read tags through the wall of the burrow or nest box without disturbing the birds. Night visits, i.e. where birds arrived and departed during the one night, could not be recorded if they did not cross the APMS in both directions.

Most birds arrived at dusk and departed at dawn on the same night or one or more mornings later. No visits or departures occurred during daylight hours, although a few birds arrived and/or departed at irregular hours during the night. A bird which arrived one night and departed the following dawn thus would have spent about eight hours ashore and a bird which remained during daylight hours would have spent approximately 32 hours ashore (depending on day length). Thus birds which change over in their incubation or guard shift each night will each spend alternately about 32 hours ashore. During the compilation of attendance statistics for this paper the first eight-hour period ashore is ignored and time is measured in days, meaning a full daylight period is spent ashore.

The breeding season was considered to start at courtship when pairs were seen together for the last period of time before the pre-laying exodus (see Fig. 1). Courtship started approximately one month (maximum 31 days) before egg laying.

The incubation period was measured from the date of laying to the date of hatching of the first egg. Nests were checked daily for eggs until the first egg was laid. No attempt was made to determine time of laying of the second egg to avoid undue interference. We assumed that for each nest incubation started one day after the first egg was laid. The guard period was taken to end at the last date a parent remained with the chick during the daytime.

Those pairs which raised at least one chick to fledging stage were considered successful. A failed nest was one in which an egg was laid but no chick was fledged.

During the incubation and the chick-guard periods parent birds alternated attendance at the nest. While one bird attended the eggs or chick the other foraged at sea. Thus incubation shift and foraging trip duration are complementary events. Where the focus is on the activity at the nest during incubation the event is referred to as the 'incubation shift'. Similarly when the focus is on foraging the event is referred to as 'foraging trip duration'.

Mean length of incubation shift (I) of both parents, as related to the day of hatching (d_0), was calculated for the 1995/96 season. The shift length was recorded on the last day before the relieving mate returned to the nest.

$$ I = \frac{\sum_{n=1}^{48} (L_n)}{S_d} $$

L = the length of each incubation shift completed on day d
S_d = the number of incubation shifts completed on day d
S_{dmax} = 48 i.e. the total number of shifting nests in a day
d = the day on which the change over of partners was observed, i.e. had occurred on the previous night
d_0 = the day of hatching and d ranges from d_0 to d_{-36}

Logistic regression analysis (McCullagh & Nelder 1983) was used to compare several variables against successful or failed breeders. Results are given as mean ± standard deviation.

RESULTS

Breeding season

The first egg was laid on 4 October 1995 and laying was essentially completed by 31 October 1995 when 49 nests had eggs, three females laid in November and one in December (Fig. 1). Two nests which failed had a second clutch which also failed (Fig. 1, nests 22 and 47). All chicks had fledged by 2 February 1996.
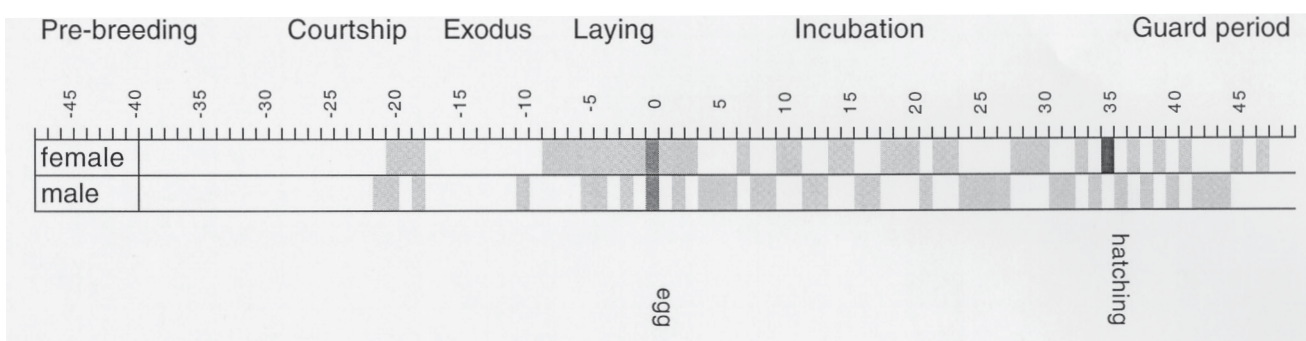

Fig. 2. *Pattern of attendance of a pair of Little Penguins from first arrival to the end of the guard period. Post-guard period is not shown. The pair represented is from nest number 1 of Fig. 1. The scale at the top represents the number of days before and after laying which is day zero. Presence ashore is in grey and black for laying and hatching date.*

Attendance patterns

Figure 1 shows the attendance patterns from 28 June 1995 to the end of the guard phase in the 1995/96 season in chronological order of laying. Attendance patterns of the adults after the guard period are not shown although the chicks were monitored daily to determine breeding success. Most of the deaths occurred after the chick-guard period.

It can be seen by focusing on the patterns of attendance at the nest (Fig. 1) that six phases are discernible. Four occur leading up to laying, namely pre-breeding, courtship, the pre-laying exodus and pre-laying which are followed by incubation and the chick-guard period. These phases are summarized diagrammatically in Figure 2.

Attendance before laying

Birds of both sexes made occasional visits to the colony during the winter non-breeding period. Rarely were both members of the future breeding pair present at the same time (Table 1).

The courtship period began approximately one month (maximum 31 days) before egg laying and lasted on average five days for females and 5.5 days for males (range 1–9 days). Males arrived earlier than did females in 60% of the cases. Males and females arrived at the same time in 25% of cases and only 15% of females arrived earlier than males in the colony. After courtship the females departed, i.e. a pre-laying exodus which lasted 10.6±3.2 days. The males also returned to the sea but for a significantly shorter period of 9.2±3.0 days ($t_{91} = 2.23$, $P = 0.028$) tending to leave later and return earlier than their partner. Following the pre-laying exodus 66% of males returned on the same day or one to two days ahead of the females (n = 52 males). One pair was recorded only on the day of laying (nest 34, Fig. 1) and two males were recorded only after laying date (nests 35 and 41, Fig. 1). They may have stayed in another burrow outside the study area during the courtship and pre-egg periods or made only night visits to the colony and were not ashore during the day.

The females remained ashore 5.6±3.1 days during which time a clutch of two eggs was laid, the first egg being laid 4.9±2.8 days after arrival. The male stayed in attendance 4.4±3.5 days and was usually absent on the morning after the first egg was recorded.

Incubation period

Incubation lasted for 35.5±1.7 days (range 31–40 days) which was slightly shorter than that previously estimated for Phillip Island (Reilly & Cullen 1981) but similar to Tasmanian birds (Hodgson 1975). The incubation period was the same irrespective of whether the birds later failed or were successful. The wide range in incubation period is attributed to interrupted incubations. Eleven nests had eggs unattended from one to six or more days. Four of these nests had eggs which hatched although they were left unattended from one to six days which were not consecutive. Eggs which were unattended for more than three days showed an increased incubation period and those unattended for periods longer than six days did not hatch (n = 7 nests, Fig. 1).

Figure 3 shows the average length of each incubation shift as related to the point of hatching. The shift length is recorded on the last day before the relieving mate returned to the nest. The shift duration was two to three days for the first half of the incubation. From about 17 days before hatching the shift duration increased to four to five days or more before decreasing again to a shift duration of one to two days, three days before hatching. It was noted that on 1–2 November there appeared to be a change from short to long incubation shifts irrespective of the laying date (Figure 1).

Individual birds made on average 5.6 incubation shifts which lasted on average of 3.4 days. There was no significant difference between males and females in the length of their incubation shifts (Table 1). However, successful breeders (males and females) had shorter shifts during incubation than did failed breeders (Table 2). It was found that number of foraging trips and length of incubation shifts were significantly different between successful and failed breeders (Table 3).
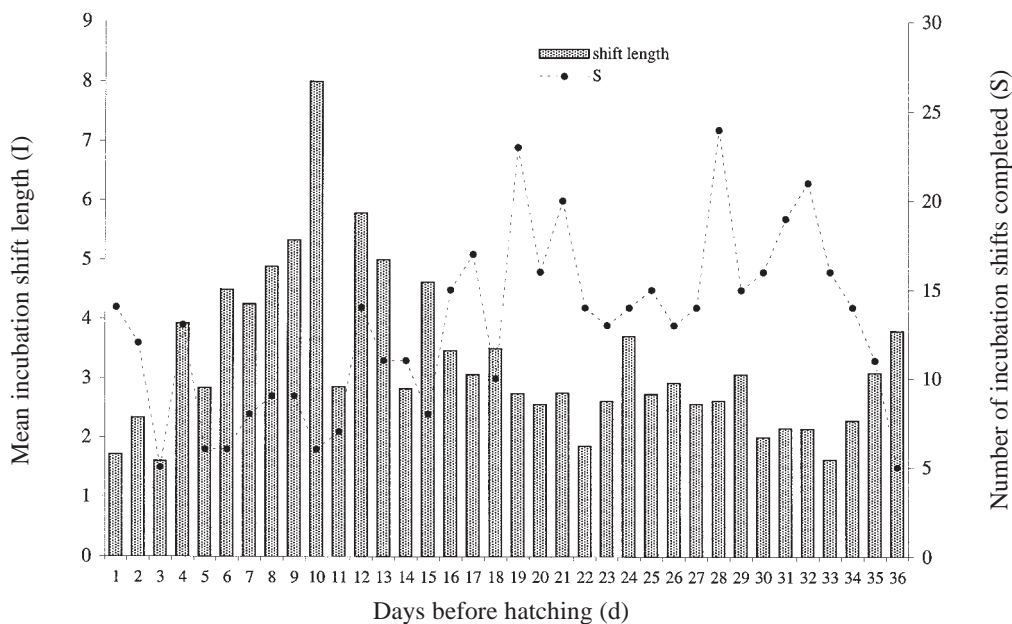

Fig. 3. *Mean length of incubation shifts (I) as related to the day of hatching (d_0). The shift length is recorded on the last day before the relieving mate returned to the nest. Data are reported for both members of the pair.*

TABLE 1

Comparison of attendance data between male and female Little Penguins at Phillip Island, 1995/96

Variable	Females			Males			Analysis of variance		
	Mean	S.D.	n	Mean	S.D.	n	t value	F value	P
Total period ashore before laying (days)	11.2	5.36	53	14.8	8.00	55	2.74		0.007
Number visits before laying	3.1	1.47	52	4.5	2.60	55	3.38		0.001
Length of incubation shifts (days)	3.4	2.25	49	3.5	1.25	54	0.25		0.806
Number of foraging trips during incubation	5.7	2.02	52	5.6	2.00	54	0.27		0.787
Length of chick-guard shifts (days)	1.3	0.76	53	1.1	0.23	47		11.09	<0.001
Number of foraging trips during chick guard	5.7	1.66	53	5.8	1.61	47	0.19		0.850
Breeding age (years)	6.4	3.25	42	7.3	3.41	41	1.18		0.240

TABLE 2

Comparison of attendance data between successful and failed breeding Little Penguins

Variable	Success			Failure			Analysis of variance		
	Mean	S.D.	n	Mean	S.D.	n	t value	F value	P
Length of visit before laying (days)	3.6	1.49	38	3.9	1.98	56	0.79		0.435
Number visits before laying	4.0	1.35	38	3.9	2.59	56		3.69	<0.001
Laying period (days)	4.7	3.26	38	5.5	3.37	56	0.63		0.524
Incubation period (days)	35.7	1.39	38	35.1	1.84	56	1.21		0.230
Length of incubation shifts (days)	2.7	0.80	38	3.7	1.17	56	3.22		0.002
Number of foraging trips during incubation	7.1	1.80	38	4.9	1.41	56	6.96		0.001
Chick-guard period (days)	14.8	2.59	38	14.3	4.07	56		2.47	<0.050
Length of chick guard shifts (days)	1.1	0.23	38	1.2	0.72	54		9.42	<0.001
Number of foraging trips during chick guard	6.0	1.13	38	5.5	1.80	54		2.55	<0.005
Breeding age (years – transformed data)	7.5	3.10	32	6.4	3.44	51	2.11		0.038

Chick-guard period

Parents guarded their chicks for an average of 14.5 days (range 8–25 days). Females spent more time ashore with their chicks than did males but both made the same number of foraging trips (Table 1). Successful parents made more trips and spent less time ashore (Table 2). Failed breeders tended to have much higher variance values as reflected in the F-test ratio although both groups had similar means (Table 2).

Breeding success and age

Breeding success for the 1995/96 season was particularly low. The number of eggs per pair averaged 1.88 from which 0.83 chicks hatched and 0.37 fledged per pair. This was a poor breeding season compared with an average of 0.8 chicks fledged per pair for the 20 previous seasons at Phillip Island (Dann & Cullen 1990).

Figure 4 shows the distribution of breeding birds by age class. About 67% of the breeding birds were between three and eight years old. These age classes agree with the age distribution of successful breeding birds per lifetime reported by Dann &

TABLE 3

Within-sex comparisons between successful and failed breeders using a logistic regression analysis (McCullagh & Nelder 1983). Asterisks denote significance to the 0.05 (*), 0.01(**) and 0.001(***) levels

Variable	Females	Males
Number of foraging trips during incubation	***	***
Length of incubation shifts	**	**
Attendance before laying	*	n.s.
Number of foraging trips during chick guard	n.s.	n.s.
Number of visits before laying	n.s.	n.s.
Length of chick-guard shifts	n.s.	n.s.

Cullen (1990). Successful breeders were on average one year older (Table 2) and laid eggs two weeks earlier ($t_{108} = 4.07$, $P = 0.0001$) than birds which failed. There was no age difference between female and male breeders (Table 1).
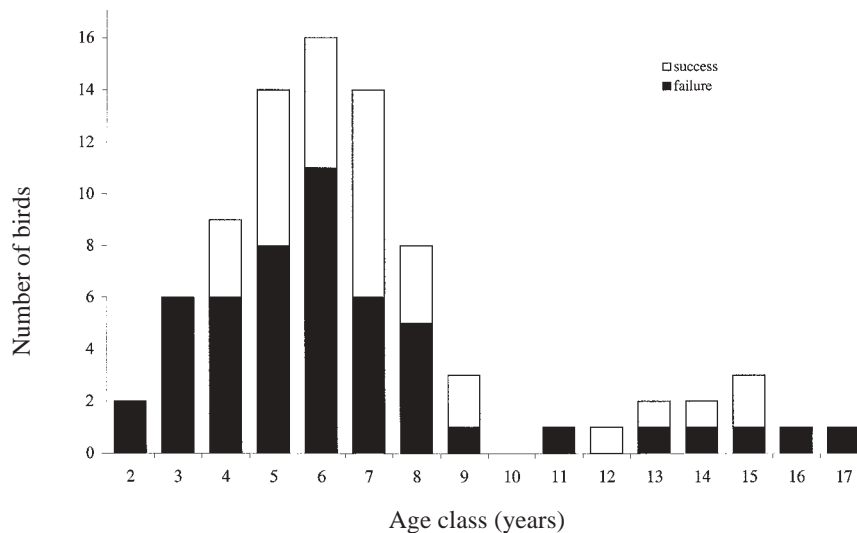
Fig. 4. *Age-class frequency distribution of successful and failed breeding birds.*

DISCUSSION

This paper presents a detailed investigation of the attendance pattern of male and female Little Penguins from the time of first arrival at the beginning of the breeding season to the end of the chick-guard period. We have noted that courtship is separated from the laying period by a pre-laying exodus for males and females and that the period of absence of females during this exodus is on average 10 days.

The incubation period from laying to hatching was 35.5±1.7 days (n = 48 nests).The period was lengthened in the few instances where incubation was interrupted intermittently. The incubation period was similar to the 33 to 37 days range (n = 7) reported for Phillip Island by Reilly & Balmford (1975) who measured incubation from the laying of the second egg to hatching of the first egg.

Female versus male attendance

Before egg-laying (including the pre-breeding period), males spent 24% (about four days) more time ashore and they arrived early at the colony for the courtship; about four weeks before laying date. Both males and females went to sea after courtship for the pre-laying exodus and then the male returned first for the laying period. After the laying period there was no difference in the attendance pattern between the sexes. These differences in attendance patterns occur during the pre-egg periods because males and females are engaged in different activities. Males need to be in the colony as often as possible to defend territories and possibly to reduce the risk of losing paternity (Chiaradia 1999). On the other hand, females should be at sea to accumulate energy to cope with the laying period. After laying, both sexes are involved in the same activity and share common tasks; therefore they have similar attendance patterns.

Incubation shifts

The duration of incubation shifts varied but on average took 3.4 days which is within the range of one to eight days recorded at Bruny and Phillip Islands (Marchant & Higgins 1990). These observations differ markedly however from data reported by Kinsky (1960), who from limited periods of observation, reported that shifts lasted only hours with females conducting more of the incubation. We concur with Williams (1995) who commented that Kinsky's (1960) results may be unusual.

The Little Penguin, in keeping with other species of penguins and seabirds, must coordinate its foraging trips between partners so that one parent is available to feed the chick at hatching. This means that no matter how the incubation foraging trips vary over the 35-day incubation period the birds must reduce the duration of their trip as hatching approaches. Our results suggest that in the Little Penguin both internal (hormonal) and external (environmental) factors are involved in the determination of length of incubation shift. These factors influence the foraging bird rather than the incubating partner since this bird has the freedom to determine when the foraging period (and hence the incubation shift of its partner) must end.

The pattern of incubation shift duration shown in Fig. 3 presumably has a physiological basis because the changes shown relate to the point of hatching even though the actual date of hatching is spread over a six-week period. Davis *et al*. (1995) showed for Adélie Penguins *Pygoscelis adeliae* that high concentrations of progesterone occur in males and females just before hatching and suggest that even if it is not progesterone that precipitates the return of the penguins it may be at least associated with whatever triggers their return. A hormonal mechanism similar to this may operate in Little Penguins. It is possible that the increase in foraging-trip duration in the second half of incubation occurs at a time when blood progesterone levels are low and that the decrease in foraging trip duration at the end of incubation is brought about by an increase in this hormone.

The observation that the length of incubation shifts tended to increase from 1–2 November for most pairs irrespective of date of laying suggests that this change was related to environmental conditions. Possible explanations include the active movement of prey away from the immediate foraging zone or changes in the environment. All birds reverted to daily foraging trip at hatching. This event may not happen every year because many factors could affect prey distribution and breeding chronology (Dann 1992, Mickelson *et al*. 1992).

Guard period

Chicks were brooded for a total period averaging 14.5±3.6 days (range 8–25 days). This is considerably shorter than the three weeks suggested by Stahel & Gales (1987) and the period of 10–21 days concluded by Kinsky (1960). Williams (1995) noted without reference that this period lasts 20–30 days. It is likely that the guard period will vary considerably between seasons and between districts since only one member of the pair is available at a time to collect food and the chick must be raised to sufficient size to gain independence. The availability of food, its proximity to the colony and the prevailing weather conditions presumably will all influence the period the chick is guarded. Length of the breeding season could vary from a bad to a good year. This variation is more noticeable during chick-rearing than during incubation. Other sea birds such as the Guillemot or Common Murre *Uria aalgae* can raise their chicks in a shorter period of time (Murphy 1995) in a good year when the food is plentiful.

A day trip for Little Penguins means a foraging area of about 8–15 km radius from the burrow (Weavers 1992, Collins *et al.* 1999). Using birds with radio transmitters, Collins *et al.* (1999) found that chick fledging, i.e. breeding success, was associated with frequency of trips. Birds which undertook short trips were more successful than were those who made longer trips. Short trips could then indicate that food was available close to the colony during chick rearing. Differences between successful and failed birds and females and males for this period are discussed in the next three sections.

Successful versus failed breeders

Only one-third of the study population bred successfully, i.e. they managed to fledge at least one chick. Almost all successful breeders laid their eggs prior to 15 October, whereas more than 50% of failed breeders laid eggs after this date (Fig.1).

Reilly & Cullen (1981) noted that for different seasons the later the onset of breeding the poorer breeding success was likely to be. We have observed further that for the 1995/96 season at least, which commenced later than usual (Reilly & Cullen 1981), that on average the earlier breeders were more successful. Successful pairs had shorter incubation shifts and undertook more foraging trips than failed birds during incubation and chick-guard period, respectively. This suggests that these birds were able to forage more efficiently than their later breeding counterparts. It is interesting to note that the duration of foraging trips increased from about 1 November. This suggests that food became generally unavailable at that time even to birds which earlier apparently had no difficulty in foraging.

The reason why some birds were able to breed more efficiently than others may be related to their age. We found that successful breeders were on average one year older and thus more experienced than were failed breeders. Moreover, successful breeders laid eggs about two weeks earlier than did failed breeders. Length of shifts and number of foraging trips during incubation were the most distinctive variables to identify the difference between successful and failed breeders. A similar pattern has been observed for King Penguin *Aptenodytes patagonicus* where a later laying date resulted in longer incubation shifts and breeding failure (Weimerskirch *et al.* 1992, Jouventin & Lagarde 1995).

Implications for monitoring

Several authors have suggested that seabirds may be used to monitor the abundance of fish stocks which form their prey (see review in Montevecchi 1993) or conversely to measure the effects of a harvest of prey on their predators (Cairns 1987, Croxall *et al.* 1988). The application of these ideas needs careful consideration since at best the measure would be one of availability of prey to predator rather than the absolute abundance of prey. Many factors are known which limit the availability of prey to the predator, including prey density, prey size, visibility, sea state, etc. Further variables which may be used as the indicators of prey availability vary enormously in their response time: e.g. foraging trip duration (attendance pattern). The onset of breeding for instance may integrate the availability of food over the several preceding months.

The present study was initiated as a first step in assessing the use of the Little Penguin as an indicator of change in the availability of prey in the marine ecosystem around Phillip Island.

The observation that attendance patterns varied between successful and failed birds, that earlier breeding birds were more successful and that the attendance pattern for the whole colony could change at much the same time suggest that the Little Penguins are responding to changes in the availability of food within the foraging zone. Thus attendance patterns as measured during this study may provide a useful tool for monitoring the availability of the major prey items in the foraging zone. The degree to which foraging patterns reflect the abundance of prey, as distinct from its availability, in the foraging zone or adjacent areas needs to be determined. The attendance patterns may be a variable which is particular responsive to change since birds only visit ashore during dusk or darkness, therefore a delay of few hours in obtaining sufficient prey will delay by 24 hours return to the colony to relieve a partner or to feed a chick.

These results are based on only one breeding season. Little Penguins have a high year-to-year variation on onset of the breeding (Dann 1992) and reproductive output (Dann & Cullen 1990) which may indicate that differences between years are likely to be great. A monitoring programme implies a continuous long-term study (Furness *et al.* 1993). The monitoring of bird attendance at the colony combined with radio-tracking of birds with known breeding histories should provide a tool for management of the Little Penguin population of Phillip Island.

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