

CHANGES IN DEPTH UTILIZATION IN RELATION TO THE BREEDING STAGE: A CASE STUDY WITH THE KING PENGUIN *APTENODYTES PATAGONICUS*

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SUMMARY

CHARRASSIN, J.-B., BOST, C.-A., PÜTZ, K., LAGE, J., DAHIER, T. & LE MAHO, Y. 1999. Changes in depth utilization in relation to the breeding stage: a case study with the King Penguin *Aptenodytes patagonicus*. *Marine Ornithology* 27: 43–47.

The impact of breeding constraints on foraging strategies of penguins has been poorly studied. We examined during two years the foraging behaviour of King Penguins *Aptenodytes patagonicus* during the incubating, brooding and crèching periods at the Crozet Islands, southern Indian Ocean. In this species, the non-synchronized breeding cycle makes possible the simultaneous study of foraging behaviour at two breeding stages, thus allowing a comparison of different foraging activities at constant food availability. Diving behaviour was assessed using time-depth recorders. When compared with birds with eggs, birds at the brooding stage dived deeper and spent more time at greater depth in summer, whereas their foraging trip duration was halved. In autumn, foraging trip duration, depth attained and diving frequency to depth >100 m for birds with small and large chicks were generally greater than those observed in birds foraging in summer. The significance of these changes is discussed with respect to breeding requirements and food availability.

INTRODUCTION

Seabirds experience extensive changes in time and energy demands during breeding (e.g. Ricklefs 1983), and this seems particularly true for the most oceanic species, which forage far at sea throughout their breeding cycle (Salamolard & Weimerskirch 1993). After the Emperor Penguins *Aptenodytes forsteri*, King Penguins *A. patagonicus* are the most oceanic species of penguins (Jouventin *et al.* 1994, Kooyman *et al.* 1996) and as such there is increasing interest in understanding their foraging strategies (Kooyman *et al.* 1992, Jouventin *et al.* 1994, Bost *et al.* 1997, Handrich *et al.* 1997, Pütz *et al.* 1998). However, few studies have yet focused on the influence of the breeding stage on foraging strategies. During the incubation period of the King Penguin each parent alternately incubates and restores its body reserves in two to three week foraging trips, ranging as far as 300–500 km from the colony (Bost *et al.* 1997). After hatching, the parental energy demand increases greatly since the chick must be provisioned regularly. As a result, more food must be gathered by each adult but over a shorter period of time (1–2 weeks, Weimerskirch *et al.* 1992).

In this study, we examined how changes in energy requirements of King Penguins breeding at the Crozet Islands, southern Indian Ocean affect depth utilization. At this locality, the breeding cycle of the King Penguin is spread over more than 13 months and the laying period lasts from mid-November to mid-March (Weimerskirch *et al.* 1992). Incubating or brooding birds are thus present at the same time in the colony (Jouventin & Lagarde 1995). This makes possible the simultaneous study of birds at different breeding stages but having to contend with the same food availability at sea. We compared simultaneously: (1) the diving activity of birds at the

incubating or at the brooding stage during summer, and (2) the diving activity of birds with small chicks or with crèched chicks during autumn. To assess how brooding a small chick during periods of high or low food availability influences the foraging activity, we also compared the depth utilization of birds at the brooding stage in summer and in autumn.

METHODS

Field work took place during the 1993 and 1995 breeding seasons at Possession Island, Crozet Islands (46°25'S, 51°45'E). The study was located in the 'Grande Manchoitière' colony (40 000 breeding pairs, Weimerskirch *et al.* 1992). In January–February 1993 (summer), the diving behaviour of eight birds at the incubating stage and of six birds at the brooding stage was investigated using time-depth recorders (TDRs) as described in Charrassin *et al.* (1998). Data were recorded at 32–120 s sampling intervals. In 1995, 'MK5' customized TDRs (Wildlife Computers, USA; 95 mm long × 38 mm wide × 15 mm high and c. 70 g) logging at sampling intervals of 5 s were used to investigate the diving behaviour of four groups of birds. They consisted of four individuals at the incubating and four individuals at the brooding stage in January–February (summer), and four individuals at the brooding stage and four individuals with crèched chicks in March–April (autumn). Briefly, birds of known status leaving the colony were caught after the egg/chick exchange occurred and devices were fitted in a lower back position to reduce hydrodynamic drag (Bannasch *et al.* 1994) using a small grid glued under the feathers. When comparing summer birds at the incubating and at the brooding stages, or when comparing autumn birds with brooded or crèched chicks, effort was made to deploy the TDRs on birds

foraging simultaneously in order to record the diving activity under as comparable as possible at-sea food conditions.

Depth data were recorded with long sampling intervals in 1993 (32–120 s), and with short sampling intervals in 1995 (5 s). Because a long sampling frequency may result in significant loss of information in the dive profiles (Boyd 1993, Wilson *et al.* 1995), data were analysed with custom-written software following two approaches. First, the proportion of time spent per 10-m depth intervals has been calculated for birds of the two years, because time-at-depth patterns are not influenced by the sampling frequency (Wilson *et al.* 1995). Second, a more detailed dive-per-dive analysis was conducted in 1995 because depth data were recorded at a sampling interval short enough to use this method (Boyd 1993) and the deep diving frequency was calculated. For this purpose, the number of dives >100 m performed by each penguin during its foraging trip has been normalized to the number of hours of daylight available over each foraging trip. For each day of foraging, daylight duration was determined as the interval between the first and the last dive (>100 m) of the day, since penguins dive deeply exclusively from dusk to dawn (Wilson *et al.* 1993).

RESULTS

General foraging characteristics

Foraging dates, trip duration and percentage time spent diving are given for each group in Table 1. In summer, incubating birds foraged for longer than birds with small chicks both in 1993 ($U = 0$, $P < 0.05$, Mann-Whitney U-test, Charrassin *et al.* 1998) and in 1995 ($U = 0$, $P < 0.05$). In autumn 1995, birds with small and crèched chicks made foraging trips of

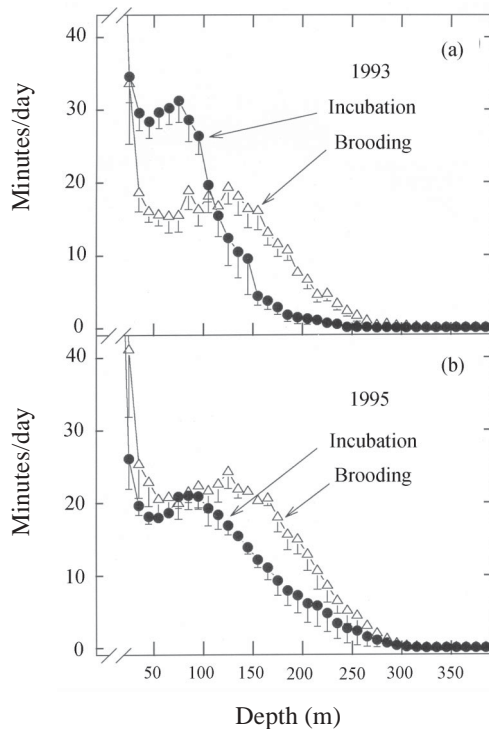


Fig. 1. Time spent per 10-m depth interval (>20 m) expressed in minutes per day at sea for incubating ($n = 8$) and brooding ($n = 6$) King Penguins in summer 1993 (a) (adapted from Charrassin *et al.* 1998) and in summer 1995 (b) (J.-B. Charrassin unpubl. data). Values are means \pm SE.

similar durations ($U = 9$, $P > 0.05$), but which were in both cases longer than for birds either at the incubation or at the brooding stage during the summer of the same year. Percentage time spent diving did not differ among groups ($H = 4.36$, $P < 0.05$, Kruskal-Wallis test).

In summer 1995, mean foraging trip duration (\pm SD) of equipped brooding birds (9.5 ± 1.7 days, $n = 4$) was significantly longer ($U = 4$, $P < 0.05$) than that of device-free birds (6.8 ± 1.9 days, $n = 8$). However, the penguins investigated continued to breed normally after the experiment, and within each year, birds studied at the different breeding stages were encumbered with the same type of device, allowing a reliable comparison of their diving behaviour.

Time-at-depth patterns

The percentage time spent per 10-m depth interval has been calculated for each individual and average values for each group are given in Figures 1 and 2. In both summer 1993 and 1995, brooding birds spent more time at greater depths than incubating birds (Fig. 1). Mean maximum depths attained by King Penguins during the incubation and the brooding periods were 205 ± 37 m and 280 ± 38 m in summer 1993, respectively (Charrassin *et al.* 1998), and 283 ± 28 m and 299 ± 21 m in summer 1995, respectively.

In autumn 1995, no difference in time-at-depth patterns was observed between brooding birds and birds with crèched chicks (Fig. 2). Birds at this time of the year exhibited the same time-at-depth pattern as birds brooding a chick earlier in the season. However, maximum diving depths were the greatest in birds foraging for large chicks (326 ± 50 m on the average) and averaged 308 ± 29 m in birds brooding small chicks in autumn (J.-B. Charrassin unpubl. data).

Deep diving frequency

The diving frequencies for dives >100 m calculated for birds studied in 1995 are plotted as a function of the foraging dates in Figure 3. Significant differences are found among all groups

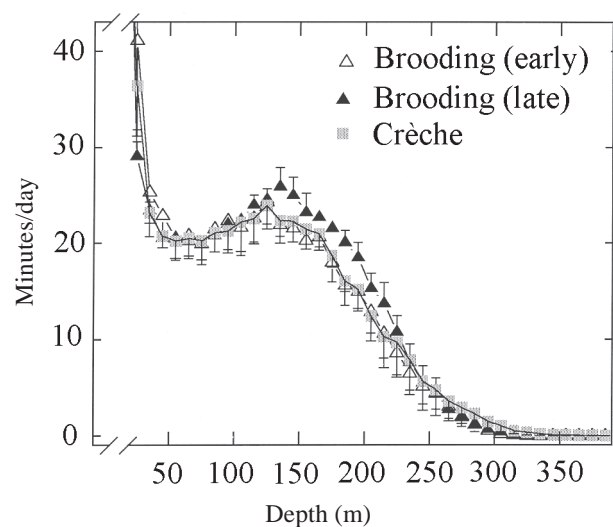


Fig. 2. Time spent per 10-m depth interval (>20 m) expressed in minutes per day at sea for King Penguins at the brooding stage early (summer) and late (autumn) in 1995, and at the crèche stage in autumn 1995 (J.-B. Charrassin unpubl. data). For each group, $n = 4$ and values are means \pm SE.

TABLE 1

Foraging dates, trip duration, and percentage time spent diving by 30 King Penguins at different breeding stages in 1993 and 1995 at the Crozet Islands

Bird no.	Incubating 1993*		Brooding 1993*		Incubating 1995**		Brooding 1995**		Brooding late 1995**		Crèche 1995**	
	Foraging dates	% time diving	Foraging dates	% time diving	Foraging dates	% time diving	Foraging dates	% time diving	Foraging dates	% time diving	Foraging dates	% time diving
1	11–25 Jan	47.9	25–30 Jan	36.9	21 Jan–3 Feb	42.9	8–18 Feb	54.7	19 Mar–25 Apr	45.8	4–24 Mar	52.2
2	13–24 Jan	45.2	23–28 Jan	49.6	27 Jan–9 Feb	42.7	18–28 Feb	60.5	20 Mar–28 Aug	53.9	9 Mar–18 Apr	47.0
3	15–30 Jan	35.3	29 Jan–6 Feb	51.1	31 Jan–19 Feb	41.4	12–23 Feb	36.2	22 Mar–3 May	46.8	18 Mar–21 Apr	43.0
4	16–30 Jan	47.3	1 Jan–8 Feb	60.6	31 Jan–20 Feb	50.5	24 Feb–3 Mar	66.0	29 Mar–8 Apr	64.0	23 Mar–27 May	50.1
5	20 Jan–3 Feb	51.7	7–14 Feb	39.1								
6	21 Jan–4 Feb	48.6	9–14 Feb	63.8								
7	23 Jan–10 Feb	42.1										
8	03–16 Feb	53.8										
Mean	14.1 ^a	46.5	6.2 ^a	50.2	16.0 ^a	44.4	9.5 ^a	54.4	62.5 ^a	52.6	39.8 ^a	48.1
SD	2.0 ^a	5.8	1.3 ^a	10.9	3.5 ^a	4.1	1.7 ^a	12.9	58.2 ^a	8.4	18.8 ^a	4.0

* adapted from Charrassin *et al.* (1998)

** J.-B. Charrassin (unpubl. data)

^a trip duration (days)

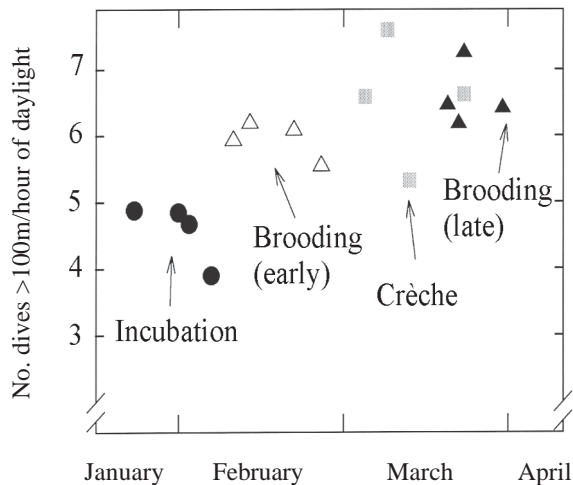


Fig. 3. Deep diving frequency (number of dives >100 m performed per hour of daylight) in King Penguins at different breeding stages in summer–autumn 1995. Data are plotted as a function of the date of departure at sea (J.-B. Charrassin unpubl. data).

($0 \leq U \leq 0.5$, $P < 0.05$) except between birds with small chicks foraging in summer and birds with large chicks foraging in autumn ($U = 4$, $P > 0.05$), and between birds foraging for small and large chicks in autumn ($U = 6$, $P > 0.05$). Average diving frequencies ranged from 4.6 dives per hour of daylight in incubating birds to 6.6 dives per hour of daylight in breeders with small chicks in autumn (J.-B. Charrassin unpubl. data).

DISCUSSION

This study has shown that time-at-depth utilization is influenced in King Penguins by both their breeding stage and the seasonal changes in food availability between summer and autumn. During the two summers of the study, King Penguins at incubation and brooding stages showed reproducible differences in time-at-depth patterns and colony attendance, suggesting that two distinct foraging tactics are involved during these breeding stages. As previously described for the Crozet Islands (Weimerskirch *et al.* 1992) and at other localities (Stonehouse 1960), King Penguins at the brooding stage made shorter foraging trips than during incubation. Interestingly, birds with small chicks dived deeper and spent more time at greater depths than did those incubating. Since both groups of birds were studied simultaneously, this suggests that differences observed in the foraging behaviour are related to the breeding stage rather than to seasonal changes in food availability. Studies using satellite-tracked King Penguins at the Crozet Islands have shown recently that birds either at the incubating or the brooding stage forage in the same oceanic areas in January–February (Jouventin *et al.* 1994, Bost *et al.* 1997). King Penguins preferentially exploit the Antarctic Polar Front region (50–51°S) at that time (Bost *et al.* 1997), where they feed mainly on myctophid fish (Cherel & Ridoux 1992, Bost *et al.* 1997). Distances to the feeding grounds (*c.* 400 km, Bost *et al.* 1997) are thus comparable for birds of both groups. However, chicks must be fed regularly, while incubating penguins can fast for prolonged periods (Cherel *et al.* 1993). This implies that less time is available to feed at the optimal foraging zone for birds with small chicks when compared to

birds with eggs. Deeper dives by brooding birds may be a means for parents to gain access to more highly productive water strata. Indeed myctophid fish are found with increasing density with increasing depth (Zasel'sliy *et al.* 1985, Perissonotto & McQuaid 1992, Duhamel 1998) and penguin feeding success may increase correspondingly. This may help the parents who have a limited time in the optimal foraging zones to augment chick provisioning (Charrassin *et al.* 1998).

In autumn birds with crèched chicks had a much longer trip duration than did birds with small chicks foraging in summer, and, although this was not statistically significant, they tended to have a greater diving frequency. Foraging effort seems thus at a maximum during the crèching period. High diving frequencies and great diving depths were equally observed in birds with a small or large chick foraging simultaneously in autumn. This strongly suggests that changes in energy requirements due to the age of the chick do not influence the parents' foraging effort. After the end of the brood stage both parents forage independently to feed the large chick which must put on substantial fat reserves before winter (Cherel *et al.* 1993, van Heezik *et al.* 1993). By contrast, less food is provided to a small chick, but since it cannot be left unbrooded, only one parent can forage at a time.

The large increase in trip duration in birds with a chick of any age foraging in autumn suggests a reduced foraging success at sea at this period (Le Maho *et al.* 1993). Myctophid fish migrate to a greater depth in autumn and seem less accessible to surface predators (Kozlov *et al.* 1991, Sabourenkov 1991). King Penguins are diurnal foragers (Wilson *et al.* 1993, Pütz & Bost 1994). Together with the autumnal drop in prey availability (Adams & Klages 1987, Le Maho *et al.* 1993), the reduction of daylight time with advancement of the season may have forced foraging penguins to make more dives and to extend the duration of their foraging trips.

Fifty to sixty percent of successful breeders of a given year attempt to breed again late in the season of the next year (Jouventin & Lagarde 1995) but their breeding success is only 1–2% at the Crozet Islands. As a consequence, the questions as to why these birds attempt to breed and what are the costs/benefits of these late breeding attempts have been raised (Weimerskirch *et al.* 1992, van Heezik *et al.* 1994, Olson 1996). Our comparison of depth utilization by birds at the brood stage early (summer) and late (autumn) in the season has shown that the autumnal drop in food availability is offset, to some extent, by a higher diving frequency. However, the foraging effort made by brooding birds in autumn was similar to that of birds with large chicks which were potential successful breeders. This suggests that trying to raise a small chick in autumn does not imply an extra cost compared to early breeders, as confirmed by the similar increase in body mass observed in both early and late breeders in April (Le Maho *et al.* 1993). This plasticity of foraging effort may be a key to breeding successfully in particular years of high food availability (Weimerskirch *et al.* 1992, J.-B. Charrassin unpubl. data).

The breeding cycle of the King Penguin is peculiar in that birds undergo changes in food availability throughout the 13 months of their breeding cycle. In this species, as opposed to most other penguins, the period of high energy demand (chick rearing) does not seem restricted to the summer period of optimal food availability. Studying diving behaviour and the energetics of King Penguins at other key stages of their annual cycle (e.g. moult) promises to be of interest in fully understanding their foraging ecology.

ACKNOWLEDGEMENTS

Logistical and financial support was provided by the Institut Français pour la Recherche et la Technologie Polaires and Terres Australes et Antarctiques Françaises. Centre National de la Recherche Scientifique (CNRS), PICS 162, GDRE 1069 and Université Louis Pasteur also funded this work. Y. Handrich and T. Raclot, as well as members of the 1993 and the 1995 wintering teams at the Crozet Islands, especially Yan Ropert-Coudert and G. Froget, offered generous assistance in the field. R.P. Wilson made helpful suggestions during the course of the study.

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