Abstract  Contrasting conditions at-sea are likely to affect the foraging behaviour of seabirds. However, the effect of season on the dive parameters of penguins is poorly known. We report here on an extensive study of the diving behaviour of king penguins (*Aptenodytes patagonicus*) over the bird’s complete annual cycle at the Crozet Islands. Time-depth recorders were used to record dive duration, bottom duration, post-dive interval, ascent rate and descent rate in breeding adults during different seasons in 1995 and 1996. Seasons included summer (*n* = 6, incubation; *n* = 6, chick brooding), autumn and winter (*n* = 5 and *n* = 3, respectively, chick at the crèche stage), and spring (*n* = 4, birds at the post-moult stage). In all seasons dive duration increased with dive depth, but, for a given depth, dives were longer in winter (6.8 min when averaged over the 100–210 m depth layer) than in spring (4.6 min) and summer (4.4 min). The time spent at the bottom of the dives, which probably represents a substantial part of the feeding time, was much longer in winter (2.5 min per dive for dives over the 100–210 m layer) than during other seasons (1.0–1.4 min), i.e. there was a 2.5-fold augmentation for similar diving depths. Ascent and descent rates increased with increasing dive depth, but no difference in the relationships between rates of ascent and descent and dive depth was found among seasons. Furthermore, for all dive depths, ascent and descent rates were independent of the bottom duration. In all seasons post-dive intervals increased with dive duration and with dive depth, but they were longer in spring (2.3 min for dives over the 100–210 m layer) and summer than in autumn and winter (1.6–1.8 min). The diving efficiency decreased with increasing dive depth and was higher in autumn and winter (0.22–0.29) than in summer and spring (0.15–0.18). The large increase in bottom and dive duration from spring to winter is in agreement with the seasonal drop in prey density, with penguins spending more time searching for prey. In contrast, the consistency of the vertical velocity during contrasting conditions at-sea suggests that the transit time to depth is an important component of the foraging behaviour (scanning of the water column) that is independent of the prey availability. The time budget of the penguins during diving in a fluctuating environment appears to vary primarily during the bottom phase of the dives, with bottom duration increasing with diminishing prey supplies, while post-dive intervals shorten in the same time.

Introduction

In air-breathing divers such as seabirds and pinnipeds, a dive typically consists of a descent phase to depth, a period spent at the bottom at maximum depth, and an ascent phase of return to the surface (Schreer et al. 2001). This basic pattern has been shown by numerous studies in which the hydrostatic pressure encountered by the diver was recorded as a function of time by a miniaturised time-depth recorder (TDR) carried by the animal (e.g. Kooyman et al. 1992; Chappell et al. 1993; Wilson et al. 1996; Kirkwood and Robertson 1997a; Georges et al. 2000; Rodary et al. 2000). This large body of data has allowed major inter-specific comparisons of dive performance. Briefly, body size is the main source of variation between diving species, with large species diving deeper and longer than small species. Secondly, for most species investigated so far, dive duration and vertical velocity during diving strongly increase with increasing dive depth. These patterns have been described in several reviews (e.g. Wilson 1995; Schreer et al. 2001).
However, most studies investigating dive patterns were conducted during summer, which corresponds to the period of the year when most species breed. At that time, the animals are readily accessible at the colony, their foraging trips are short, and they regularly return to the colony to feed their young. Consequently, the probability of recovering the equipment is highest in summer. In contrast, few studies have attempted to compare intraspecifically the diving behaviour over different seasons. This is probably related to logistic problems and to the limited memory size of instruments that does not allow coverage of the entire duration of the much longer winter trips. However, the marine environment shows strong seasonal changes in biological production (Foxton 1956; Clarke 1988), which can have a profound impact on the feeding ecology of predators. The winter season is characterised by a drastic drop in the marine primary production. The winter season is characterised by

Materials and methods

Animals and instrumentation

Field work was conducted in 1995 and 1996 at “La Grande Manchotière” colony, Possession Island, Crozet Archipelago (46°25’S; 51°45’E). About 40,000 pairs of king penguins (Aptenodytes patagonicus) breed in this colony, with the whole Crozet Archipelago (1 million pairs) representing ~50% of the world population (Guinet et al. 1995). The diving behaviour of 21 birds was monitored so that birds over the complete annual cycle of the king penguin were represented, as described in Charrassin and Bost (2001). Birds studied in summer (1995) were either incubating or brooding a 1- to 3-week-old chick. Birds studied in autumn (1995) and in winter (1995–1996) were caring for an emancipated chick at the creche stage (i.e. older than 6 weeks). Birds studied in spring (1996) were at the post-moulting stage; they were unsuccessful breeders from 1995 that were randomly captured just after moulting in the earliest cohort of moulting penguins. All foraging trips were performed by different individuals, except for three birds for which we studied the foraging activity at the incubating and brooding stages consecutively. TDRs deployed in summer, autumn and winter were Mk5 3.0 (95 ±8x15 mm, 70 g) (Wildlife Computers, USA), and those used at the post-moulting stage were Mk5 3.3 (110 ±38x15 mm, 90 g). The TDRs recorded hydrostatic pressure with a 2 m depth resolution over a range of 0–500 m and had a 512 kb memory. The sampling interval was 5 s in summer, and 10 s during the autumn, winter and post-moulting periods. Depth measurements were made every second day in the winter creche group to allow for complete coverage of long trips. To reduce the hydrodynamic drag (Bannasch et al. 1994), the TDRs were fitted to the lower back of the birds. Cable-ties were used to fix the TDRs to a small metal grid, which was glued to the feathers of the back with fast epoxy. Birds were flipper marked with coloured paint. After equipment, the birds were released close to the edge of the colony. All birds were freed of their devices upon their return. Maximum care was taken to reduce the stress to the birds, e.g., by covering the birds’ eyes during handling and by moving carefully.

Analysis of diving behaviour

A dive-per-dive analysis was conducted on depth data that were corrected for surface drift (range: ± 2 to 10 m) using custom-made software (Jensen Software Systems, Laboe, Germany). Only dives > 4 m were analysed, because dives < 4 m could not be reliably resolved by the instruments. Maximum dive depth, dive duration, post-dive interval, time spent at the bottom and vertical dive velocities were obtained. Post-dive intervals were calculated between consecutive deep dives (i.e. dives to ≥250 m, Roberts-Coudert et al. 2000a). Post-dive intervals lasting > 1,000 s represented < 90% in number, and were excluded from the analysis. Bottom duration was defined as the interval of time spent at a depth > 90% of the maximum depth of the dive. This depth threshold was found by comparing the “real” bottom duration, which was determined visually from the dive profiles, with calculated bottom durations using different thresholds. For 900 dives to > 50 m, recorded for three individuals, a 90% depth threshold resulted in a bottom duration equal to 95% of the “real” bottom duration. Furthermore, the average threshold given by the “real” bottom duration was 92% of the maximum dive depth. Vertical velocities were obtained during the descent phase (descent rate calculated from the surface to the beginning of the bottom phase) and during the ascent phase (ascent rate calculated from the end of the bottom phase to the surface). The diving efficiency was calculated following the equation of Ydenberg and Clark (1989): diving efficiency = bottom time/(dive duration + post-dive interval). The data post-dive interval, and vertical ascent and descent rates across seasons. The results are discussed in terms of seasonal prey availability and behavioural adjustments.