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SHORT UNDERWATER OPENING OF THE BEAK FOLLOWING IMMERSION IN SEVEN PENGUIN SPECIES

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Abstract. Videocamera recordings of seven species of penguin, Emperor (*Aptenodytes forsteri*), Humboldt

(*Spheniscus humboldti*), Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*), Gentoo (*P. papua*), Macaroni (*Eudyptes chrysolophus*) and Rockhopper (*E. chrysocome*), swimming in large aquaria revealed that birds opened their beak underwater for less than a second immediately after initiating a dive. Overall, this beak-opening occurred in 64% of the immersions but,

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in all species, was associated with quick transitions between air and water, such as in porpoising or dives that were initiated rapidly. Two hypotheses are proposed to explain this behavior: beak-opening may be a signal that initiates bradycardia, such as is observed in unrestrained diving animals, or beak-opening may be associated with chemoreception to help detect potential prey or predators.

Key words: beak-opening, captive penguins, chemoreception, diving response, immersion, physiology.

Breve Apertura del Pico en Pingüinos luego de Sumergirse

Resumen. En acuarios registramos con cámara de video a siete especies de pingüinos, *Aptenodytes forsteri*, *Spheniscus humboldti*, *Pygoscelis adeliae*, *P. antarctica*, *P. papua*, *Eudyptes chrysolophus* y *E. chrysolome*. Los registros indicaron que las aves abren el pico bajo el agua por menos de un segundo inmediatamente después de sumergirse al iniciar el buceo. En total, esta apertura del pico se registró en el 64% de las inmersiones y en todas las especies ocurrió preferentemente en situaciones de transición rápida entre aire y agua, como en "porpoising" o en buceos que se iniciaron abruptamente. Se proponen dos hipótesis para explicar esta conducta: la apertura del pico puede servir como una señal para iniciar la bradicardia, como se observa en animales buceando voluntariamente, o bien la apertura del pico podría estar asociada a quimiorrepción para detectar potenciales presas o depredadores.

All diving birds and mammals originated from a terrestrial environment but now exploit a medium that differs radically from air. These animals exploit this medium with a suite of physiological (Butler and Jones 1997) and behavioral (Thompson and Fedak 2001) adaptations. Documentation of these adaptations has followed the form of sequential hypothesis testing as well as research stemming from serendipitous observations. During testing of a beak angle sensor on captive penguins swimming in aquaria in Japan, we noted that birds frequently opened their bills immediately following head immersion and before diving. In this paper we report this behavior in seven captive penguin species and speculate on the importance this might have for these highly specialized diving birds.

METHODS

During May 2000 and February 2001, captive penguins were filmed as they swam in a $20 \times 4 \times 2.2$ m pool in Nagoya Public Aquarium, Nagoya, Japan. The behavior of three Adélie (*Pygoscelis adeliae*), three Gentoo (*P. papua*), and three Chinstrap (*P. antarctica*) Penguins, identified by bands of colored tape around the bases of their flippers, as well as the behavior of six Emperor Penguins (*Aptenodytes forsteri*) not identified individually, was documented with a digital videocamera (30 frames sec^{-1} , Handycam DCR-PC7, Sony, Japan). Birds were filmed individually during sessions that lasted for a maximum of 10 min. In addition, porpoising by one Adélie Penguin was filmed while the bird was equipped with an IMASEN data-

logger (Intermandibular Sensor; Driesen & Kern, GmbH, Kiel, Germany). This data-logger detects and measures the duration and angle of beak opening. It was set to record at a frequency of 25 Hz (for technical details of the data-logger see Wilson et al. 2002).

In a second set of experiments, 132 Humboldt (*Spheniscus humboldti*), 18 Rockhopper (*E. chrysolome*), and 2 Macaroni Penguins (*Eudyptes chrysolophus*), were filmed (using the same apparatus as used in Nagoya) swimming in a $30 \times 8.5 \times 2$ m pool during February 2001 in Tokyo Sea Life Park. Here, the number of birds swimming together was highly variable, although they tended to enter the water and swim together. In the Nagoya aquarium, an exhibit window making up one complete side of the pool allowed us to track birds for the whole period they were submerged; however, the exhibit window in Tokyo Sea Life Park covers only a portion of one of the pool's sides and it thus proved impossible to follow all dives from beginning to end.

During feeding times, video recording was complicated by the birds swimming at high speeds, often rapidly changing direction and seizing prey underwater. During analysis of the video the following variables were investigated: dive duration (from beak immersion to head emergence), beak movements (open or closed, duration of opening), and the onset of the dive, which was categorized as "surface" (bird floating at the surface with the head out of water prior to a dive), "head underwater" (bird floating at the surface with the head under the water and the beak closed) and "porpoising" (the whole body of the bird emerging from the water during a leap).

STATISTICAL ANALYSES

Trends were highlighted with a nonparametric Spearman rank correlation (r_s) and differences between species were tested using a one-way ANOVA (Sokal and Rohlf 1969). Statistical analyses were carried out using Statview version 4.57 (Statview 1996). For all tests, the statistical threshold was 0.05. All values are presented as mean \pm SD.

RESULTS

A total of 625 min of penguin swimming and diving behavior was recorded, 450 min in the Nagoya Public Aquarium and 175 min in the Tokyo Sea Life Park. The process of bird submergence was analyzed frame by frame. Totals of 98, 103, 67, 35, and 91 immersions were recorded for Gentoo, Chinstrap, Adélie, Emperor, and Humboldt Penguins, respectively. We observed beak-opening in Rockhopper and Macaroni Penguins, but due to the small sample of immersions for these species we do not analyze them further.

Birds opened their beaks during dives to feed or peck at other penguins and also immediately after immersion prior to descending through the water column. In Nagoya, six birds (two Adélie, two Gentoo, one Chinstrap, and one Emperor) were tracked for more than 10 consecutive immersions. Overall, beak-opening occurred after 64% of immersions, but a substantial percentage (23%) of birds' immersions could not be observed. This was particularly true in the smaller species, such as Adélie, Chinstrap, and Gentoo Penguins, where 28%, 25%, and 22% of the immersions

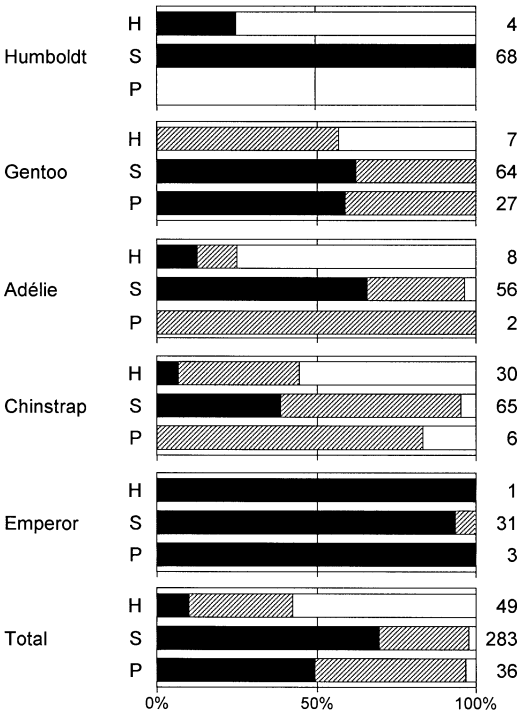


FIGURE 1. Underwater beak-opening in five species of penguins swimming in large aquaria. Proportion of immersions followed by a short beak-opening (filled bars), and proportion of immersions where birds could not be observed (hatched bars), according to immersion type: head underwater (H), surface (S), and porpoising (P).

could not be observed, respectively. Beak-opening was observed following 93% of Emperor Penguin immersions, while 7% of immersions could not be observed. In addition, beak-opening was significantly more associated with “surface” than “head underwater” immersions (Fig. 1). Although immersions were difficult to observe in the case of porpoising, due to substantial air dragged down as birds re-entered the water, beak-opening was observed following 50% of all immersions.

The frame-by-frame analysis revealed that the beak-opening occurred on average 0.16 ± 0.18 sec after the immersion of the beak and lasted for 0.52 ± 0.38 sec ($n = 193$ immersions, data for all species combined). However, there were interspecific differences in the duration of the beak-opening (Table 1). Post-hoc tests revealed that Emperor and Humboldt Penguins opened their beaks significantly longer than the three other species. Of all species, Emperor Penguins opened their beaks the longest (Table 1).

The duration of beak-opening was independent of the duration of the subsequent dive in Emperor ($r_s = 0.15, P = 0.64, n = 11$), Adélie ($r_s = 0.14, P = 0.47, n = 26$), and Chinstrap ($r_s = 0.19, P = 0.41, n = 19$) but not in Gentoo Penguins ($r_s = 0.34, P = 0.04, n = 38$). The delay between beak immersion and the start

TABLE 1. Mean delay between immersion of the beak and the onset of the underwater beak-opening, and mean duration of beak-opening, in five penguin species swimming in large aquaria.

Species	Number of immersions	Delay (sec)	Duration of beak-opening (sec) ^a
Emperor Penguin	25	0.21 ± 0.13	1.34 ± 8.68 a
Humboldt Penguin	84	0.13 ± 0.25	0.49 ± 0.22 b
Adélie Penguin	27	0.20 ± 0.10	0.35 ± 0.14 c
Gentoo Penguin	37	0.17 ± 0.12	0.29 ± 0.13 c
Chinstrap Penguin	20	0.20 ± 0.03	0.27 ± 0.08 c

^aEffect of species on duration of beak-opening: $F_{4, 189} = 133.7, P < 0.001$. Species with different letters were significantly different in post-hoc tests.

of beak-opening was significantly related to the duration of beak-opening in Gentoo, Emperor, and Adélie Penguins. In Emperor ($r_s = -0.99, P < 0.001, n = 25$) and Adélie Penguins ($r_s = -0.42, P = 0.03, n = 27$), longer delays were followed by shorter beak-openings. In Gentoo Penguins ($r_s = 0.39, P < 0.02, n = 37$), the duration of beak-opening increased with increasing delay while Humboldt ($r_s = -0.08, P = 0.45, n = 84$) and Chinstrap Penguins ($r_s = 0.09, P = 0.67, n = 20$) showed no relationship between the duration of beak-opening and the delay between immersion and beak-opening.

Data recorded by the IMASEN logger showed a clear picture of beak-opening following porpoising (Fig. 2). Based on these data, birds opened their beaks following 98% ($n = 48$) of the porpoising leaps, with beak-openings lasting a mean of 0.35 ± 0.09 sec ($n = 49$ porpoising leaps) with a mean maximum intermandibular angle of $4.6 \pm 3.0^\circ$ (range $0.7\text{--}16.5^\circ$). The duration of beak-opening immediately following submergence was positively correlated with the duration of beak-opening associated with breathing during the preceding porpoising leap (0.41 ± 0.06 sec, $r_s = 0.30, P < 0.04$). However, the maximum intermandibular angle was not related to the angle during breathing ($23.2 \pm 6.3^\circ, r_s = 0.05, P > 0.5$).

DISCUSSION

To our knowledge the short underwater beak-opening described here has not been reported previously. It seems unlikely that this behavior is associated with drinking since both field metabolic rate studies using doubly labeled water (Culik and Wilson 1992) and studies monitoring the esophageal temperature in free-ranging seabirds (Ropert-Coudert et al. 2001) suggest that penguins do not ingest significant amounts of seawater. In addition, the high energetic cost of warming ingested water (Wilson and Culik 1991), the fact that seabirds can derive all the water they need from their prey (Gabrielsen and Melhum 1987, Birt-Friesen et al. 1989), and the high incidence of this behavior all argue strongly that this behavior is not related to water ingestion. Beak-opening does not appear to be associated with the expulsion of respiratory air either, as has been

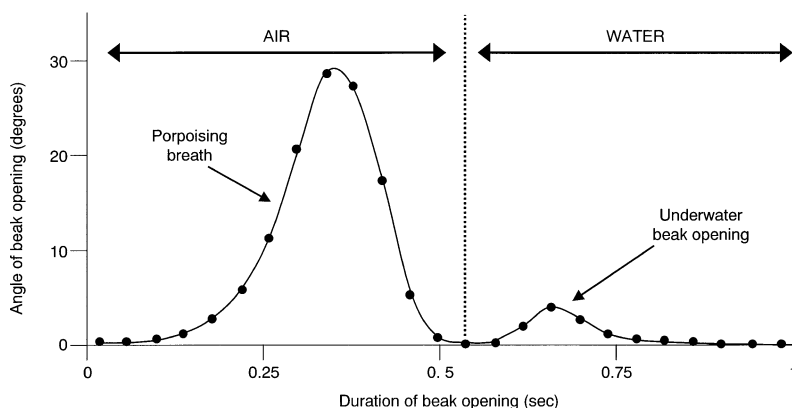


FIGURE 2. Intermandibular angle versus duration of a beak opening in the air (left) during a porpoising leap and the beak-opening directly following re-entry into the water (right) in a captive Adélie Penguin, recorded by an IMASEN data-logger.

noted in Common Eider (*Somateria mollissima*) and Tufted Ducks (*Aythya fuligula*, Butler and Woakes 1979, Hawkins et al. 2000). Air expulsion is considered to reduce upthrust, which is highest near the surface (Wilson et al. 1992), but we observed no expiratory air bubbles on video records. Finally, it also seems unlikely that birds opened their beaks in order to adjust the internal pressure in the middle ear the way human divers do, since birds in our study were swimming in the subsurface layer (maximum depth 2.4 m) and, in any event, displayed this behavior within a few centimeters of the water surface when hydrostatic pressure was minimal.

Beak-opening was observed in all of the seven penguin species investigated and all immersion types that involved a quick transition from air to water ("surface" and "porpoising") were almost invariably followed by beak-opening. The small data set collected by the IMASEN data-logger suggests that the percentage of immersions followed by a beak-opening may be even higher than our videocamera study suggested. Although there was substantial interspecific and inter-individual variability, the duration of the beak-opening appears to decrease with increasing delay between head immersion and beak-opening. This suggests that, whatever the function of this beak-opening, the extent to which it need be carried out may be reduced by long immersions of the head prior to initiating a dive. The correlations between the duration of the beak opening and the dive duration may improve if the space available for diving, particularly depth, were not so limited. Use of the IMASEN data-logger on free-living birds (Wilson et al. 2002) should help clarify this matter. Similarly, a stronger correlation may be apparent between the delay in beak-opening following immersion and the duration of the beak-opening with increased sample size. We speculate that there are two possible reasons for the observed beak-opening: that it might be related to the diving response, helping to promote bradycardia at the onset of a dive or, alternatively, birds might be tasting the water to detect chemical

traces left by prey or predators. More research on both hypotheses is urgently needed.

The absence of documentation of the short opening of beaks underwater may simply be because the event is so transient and difficult to observe. However, the ubiquitous nature of this behavior suggests that it is important. Determination of its function may well enhance our understanding of bird physiological adaptations to diving and foraging at sea and it therefore deserves further investigation.

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