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Dive Depth and Diet of the Black-vented Shearwater (*Puffinus opisthomelas*)

BRADFORD S. KEITT,[1] DONALD A. CROLL, AND BERNIE R. TERSHY
Institute of Marine Sciences, University of California, Santa Cruz, California 95064, USA; and
Island Conservation and Ecology Group, P.O. Box 141, Davenport, California 95017, USA

In general, procellariiforms have been considered to be surface and shallow-dive foragers (Brooke 1990, Warham 1990). This view has persisted despite Kuroda's (1954) demonstration that Short-tailed Shearwaters (*Puffinus tenuirostris*) and Sooty Shearwaters (*P. griseus*) have streamlined tarsi and a narrow pelvis that should make them more proficient divers than some other procellariiforms. Weimerskirch and Sagar (1996) deployed maximum depth gauges and found that Sooty Shearwaters dive to 67 m. These depths are surprising for such a proficient flier. Weimerskirch and Sagar's data corroborate Kuroda's predictions from his morphological data and challenge previous assumptions about shearwater foraging ecology. However, it is difficult to determine whether diving is widespread in shearwaters because no studies have been published on the diving capabilities of species other than the Sooty Shearwater. Here, we examine maximum dive depths and diet of the Black-vented Shearwater (*Puffinus opisthomelas*).

The Black-vented Shearwater is endemic to islands off the Pacific coast of Mexico and is the only shearwater that breeds on islands in the California Current (Everett 1988). Anecdotal observations of this species began at the turn of the century (Anthony 1896), but only recently have detailed studies been conducted on the biology of this species (Keitt 1998). Natividad Island, Baja California, Mexico, with a breeding population of about 150,000 pairs, supports most of the world population. The Black-vented Shearwater is a summer breeder with a four-month reproductive cycle that is very similar to that of the well-studied Manx Shearwater (*Puffinus puffinus*; Harris 1965, Perrins et al. 1973, Brooke 1990). At-sea observations indicate that the Black-vented Shearwater, unlike many other procellariiforms, is a near-shore forager that does not regularly make extended pelagic foraging trips (Ainley 1976).

Methods.—Maximum depth gauges (MDG) were deployed at Natividad Island between 13 May and 30 June 1998. The MDGs were constructed similar to those described in Croll et al. (1992). Briefly, lengths of Tygon tubing (15 to 18 cm) were lined with a soluble indicator (confectioner's sugar), and one end was securely tied to allow water entry only at the

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[1] Address correspondence to Institute of Marine Sciences, University of California, Santa Cruz, California 95064, USA. E-mail: bkeitt@islandconservation.org

open end. Following Boyle's law, when the MDG is submerged, water enters the open end of the tube and dissolves the confectioner's sugar to a length proportional to the maximum pressure encountered, providing a measure of the maximum depth of the dive (see Falk et al. 2000).

Breeding adults were captured at their nest burrows, marked with United States Fish and Wildlife Service leg bands, and fitted with a depth recorder attached to the contour feathers between the scapulars with a cable tie. The mass of the tube and tie was approximately 2 g (<0.6% of body mass). Depth recorders were recovered after one foraging trip (24 to 120 h after deployment), and the length of Tygon tubing with undissolved confectioner's sugar (L_d) and the total length of the tube (L_s) were measured to the nearest millimeter. Maximum depth attained during the foraging trip (D_{max}, in meters) was calculated as:

$$D_{max} = 10.08\ (L_s / L_d - 1), \qquad (1)$$

where 10.08 is a constant in meters reflecting atmospheric pressure at sea level (Burger and Wilson 1988).

We recovered 11 depth gauges during incubation and 19 during the chick-rearing stage. We obtained multiple measurements of maximum dive depth from 10 birds. Because a comparison of all maximum dive depths and dives recorded from the same birds showed the pooled variances to be similar (103.5 and 104, respectively), we treated each dive depth as an independent measurement.

We collected 20 regurgitation samples opportunistically from adult Black-vented Shearwaters during the chick-rearing period in 1997 and 1998. The birds regurgitate when handled, and samples were collected from birds caught at the colony for banding and morphological measurements. We assumed that most samples came from adults that were preparing to feed chicks, but we do not know for certain whether the birds were breeders or nonbreeders. Samples were weighed, preserved in 10% formalin, and stored in alcohol. In addition, gizzards from seven shearwaters that were killed by house cats were collected from April to June 1998. These were stored in alcohol and the contents inspected in the lab.

Regurgitation samples were sieved and all hard parts saved. Fish vertebrae were identified by comparison with known specimens by Tom Wake, Director of the Zooarchaeology Laboratory, Institute of Archaeology, University of California at Los Angeles. Contents of the gizzards were separated into otoliths and squid beaks. Otoliths were sent to Mark Lowry at the Southwest Fisheries Science Center for identification. Eric Hochberg from the Santa Barbara Museum of Natural History identified the squid beaks.

We estimated the length (mm) and wet mass (g) for the largest squid in our sample using the allometric equations from Clarke (1986) for mastigoteuthid squids:

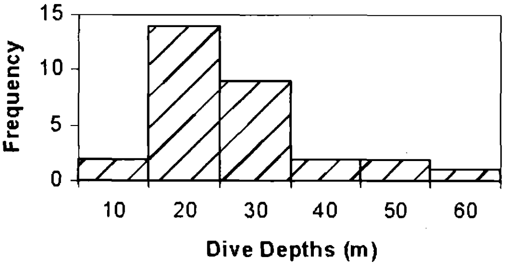

FIG. 1. Frequency distribution of maximum dive depths (n = 30) by Black-vented Shearwaters on Natividad Island, Mexico.

$$\ln(\text{wet mass}) = 0.184 + 2.88 \times \ln(\text{lower rostral length}), \qquad (2)$$

and

$$\text{mantle length} = -1.8 + 29.08 \times \text{lower rostral length}. \qquad (3)$$

Results.—We recovered 30 depth gauges from 18 shearwaters; eight birds were sampled once, nine twice, and one four times. MDGs were deployed for a mean of 3.4 ± SD of 1.9 days ($n = 30$). The mean maximum dive depth was 21 ± 11 m ($n = 30$), and the shallowest and deepest maximum dives recorded were 8 m and 52 m, respectively. The distribution of the 30 maximum depths showed that most of the dives were much shallower than the maximum dive potential for the species (Fig. 1). Dive depth and duration of MDG deployment were not significantly correlated ($r_s = 0.04$, $P = 0.82$). Birds dived deeper during the chick-provisioning period ($\bar{x} = 24.3 \pm 12.3$ m, $n = 19$) than during incubation ($\bar{x} = 16.3 \pm 4.2$ m, $n = 11$; Behrens-Fisher $t = 0.23$, df = 18, $P = 0.02$; Fig. 2).

Gizzard samples revealed that Black-vented Shearwaters fed on mastigoteuthid squid and northern anchovies (*Engraulis mordax*). Of the seven gizzards collected, three (43%) were empty and four (57%) contained squid beaks. Two of these latter four also contained fish otoliths. Most of the materials were unidentifiable fragments of squid beaks. Three of the gizzards contained a squid species in the Mastigoteuthidae. A fourth gizzard contained two identifiable specimens of *Mastigoteuthis pyrodes*, which is another species of mastigoteuthid. We calculated the wet mass of the squid with the largest intact beak to be 1.6 g and the length to be 30 mm. Additional beaks in this gizzard were too small to identify. We found nine otoliths from at least five northern anchovies in two gizzards.

We were able to weigh 9 of the 20 regurgitation

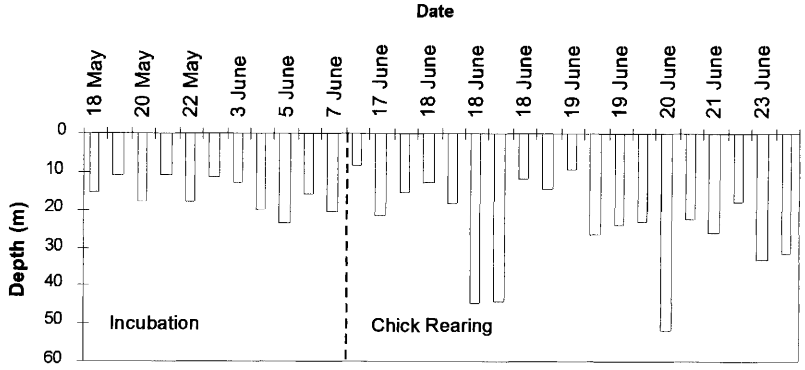

FIG. 2. Changes in maximum dive depths by Black-vented Shearwaters during the breeding season on Natividad Island, Mexico.

samples collected in the 1997 and 1998 breeding seasons ($\bar{x}$ = 43 ± 16.4 g). Twelve (60%) of the 20 samples contained almost no hard parts to aid in identification of the contents. Eight (40%) samples contained partially digested fish without heads, and six contained northern anchovies with estimated total lengths of 6 to 10 cm. Two samples contained Pacific sardines (*Sardinops sagax*) with estimated total lengths of 8 to 10 cm. One of the samples contained vertebrae from a chub mackerel (*Scomber japonicus*).

Discussion.—The first application of MDGs on procellariids revealed that Sooty Shearwaters reached depths of 67 m (Weimerskirch and Sagar 1996). Our data on maximum dive depths of Black-vented Shearwaters, a species with very different ecology than the Sooty Shearwater, further supports the morphological evidence provided by Kuroda (1954) that shearwaters are accomplished divers.

Some seabirds have much more specialized diving morphology than shearwaters. Using the allometric equation for maximum dive depth for penguins and alcids (Burger 1991; $D_{max} = 75.905\ M^{0.316}$, where M is the mass of the bird in kg), a 406-g bird like the Black-vented Shearwater would be expected to dive to 57 m. This is remarkably similar to the observed maximum dive depth of 52 m in our study, a surprising result considering that shearwaters do not share the same specialized diving morphology of alcids and penguins. A Sooty Shearwater, at 850 g, would be expected to dive to 72 m, again very close to the maximum observed depth of 67 m for this species (Weimerskirch and Sagar 1996).

It is possible that Black-vented Shearwaters maximize their diving capability by minimizing wing-surface area through molting, as proposed for Common Murres (*Uria aalge*; Croll 1990, Thompson 1998). Decreased wing-surface area results in increased wing loading and decreased flight efficiency. Unlike most species of procellariiforms, which molt outside of the breeding season (Warham 1996), Black-vented Shearwaters begin primary molt when their chicks hatch, and they continue to molt throughout the chick-rearing period (B. Keitt unpubl. data). Because the colony on Natividad Island is located close to a productive upwelling center at Punta Eugenia (Huyer 1983), Black-vented Shearwaters, which are known to forage near the coast (Ainley 1976), may encounter relatively high prey abundance close to the breeding colony (Tyler et al. 1993). Thus, unlike Sooty Shearwaters, which travel 1,500 to 2,000 km to forage during the chick-rearing period (Weimerskirch et al. 1994), Black-vented Shearwaters may have less need for efficient flight when foraging. Although primary molt may decrease flight efficiency, it is also likely to increase diving efficiency by decreasing wing drag. Thompson et al. (1998) examined remigial molt in Common Murres and suggested that primary molt in the larger alcids "reduces their wing-surface area to a size that is probably close to the optimal for underwater flight." The timing of molt in Black-vented Shearwaters also may serve to increase diving efficiency during the chick-provisioning period.

Northern anchovies and Pacific sardines were the main items found in the Black-vented Shearwater diet samples. The location of Natividad Island in an area of strong upwelling provides a highly productive foraging area within 30 km of shore (Huyer 1983, Tyler et al. 1993). Northern anchovies and Pacific sardines are the most common schooling fish in this region (Lluch-Belda et al. 1989), and it is likely that Black-vented Shearwaters are feeding on prey items with the highest availability near the colony.

In conclusion, we found that Black-vented Shearwaters, like Sooty Shearwaters, are able to forage down to 50 m in the water column. This provides support for Kuroda's anatomical evidence for diving adaptations in shearwaters. Our limited data on diet are the only data available for this poorly studied species, and they show that Black-vented Shearwaters feed on locally abundant schooling fish and mastigoteuthid squid. We found distinct temporal changes in maximum dive depths during the shearwater's breeding season. These may translate into temporal differences in prey consumption; however, we were not able to collect diet samples and diving data on the same birds at the same time. Further studies should examine these important factors simultaneously.

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